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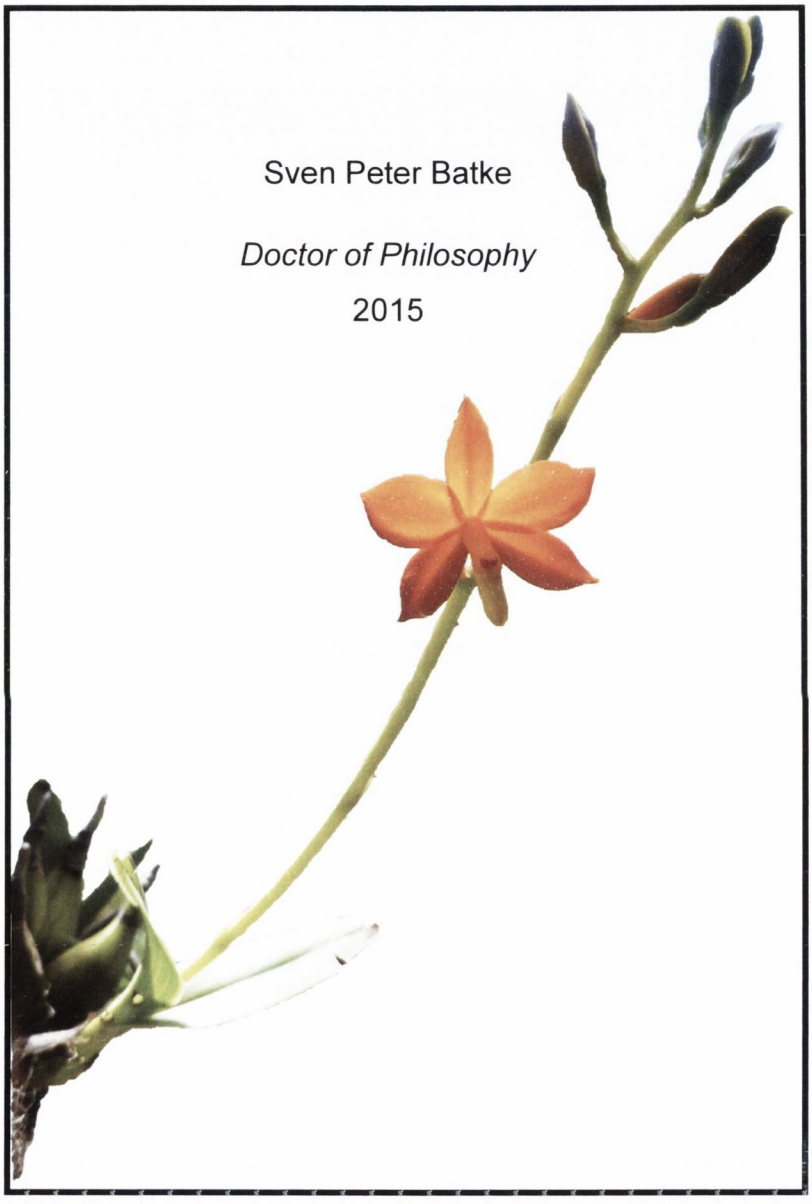
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Ecology and distribution of mechanically dependent plants along a gradient of past hurricane impact



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Doctor of Philosophy

2015

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Summary

High energy weather events have been shown to substantially affect forest community dynamics by causing structural and microenvironmental alterations to the affected stand. The degree to which forests respond to storm damage depends on the frequency, intensity and duration of the events and the susceptibility of individual trees to damage. As the microenvironment of forest canopies is closely coupled to the structural environment of the forest (e.g. canopy closure), microclimate alterations are thus likely to follow storm damage.

Mechanically dependent plants such as holo-epiphytes, hemi-epiphytes, climbers, nomadic vines, stranglers and hemi-parasites (i.e. mistletoes) are strongly dependent on the stability of the forest canopy environment. Any direct and/or indirect modification of the forest canopy as a result of storm damage (e.g. damage to the physical substrate and changes of the microclimate) may affect their diversity and composition.

The aims of this thesis were to provide baseline data on the mechanically dependent flora of Cusuco National Park (CNP), Honduras and to investigate the composition and diversity of dependent plants along a gradient of past hurricane impact and in relation to environmental and structural variables of the host tree. A hurricane model was computed that allowed the prediction of hurricane-related incidences at a mesoclimate scale for CNP. Rope-climbing techniques were employed to assess storm damage and to sample the abundance and richness of all dependent life-forms in ten 150 ×150 m plots. Data loggers were suspended for a 12-month period within individual trees, to identify differences in the microclimate among sites and among different levels within the canopy.

Eleven hurricanes were identified as having affected CNP between 1995 and 2010. However, most winds that impacted CNP reached only tropical storm strength. The model explained 73% of physical tree damage. Damage differed between tree types: Conifers had more branch damage compared to angiosperms. The vapour pressure deficit (VPD) varied along the vertical

gradient and was highest in the upper canopy and on sites that had been more impacted by hurricanes. The hurricane model explained 12% of the total variance in VPD.

A total of 7094 individuals of mechanically dependent plants from 214 species were identified. Holo-epiphytes and climbers were the most diverse life-forms. A biogeographic comparison of epiphytes in CNP to other Central American regions revealed that over 20% of all vascular plants recorded in CNP are epiphytic and that epiphytism was observed in 11% of Honduran vascular plant species. The epiphyte flora of Honduras and CNP was most similar in composition to that of Nicaragua and Belize and notably dissimilar to the floras of Panama and Costa Rica.

The diversity of dependent plants in CNP was negatively correlated with past modelled hurricane impact. The variables that explained most of the dissimilarity of the dependent plant communities among plots were VPD, elevation, aspect, slope and plot exposure (total explained variance was 44.4%). At the individual tree level, the community dissimilarity was explained by differences in host tree life-form (angiosperms versus conifers), canopy openness and hurricane damage (total explained variance was 30%). Within individual trees, the abundance of dependent plants varied with height in the canopy and with different structural and environmental variables. Abundance of species was highest in the lower canopy on sites that had been least impacted by hurricanes and highest in the upper canopy on sites that had been most impacted by hurricanes. The shifts in abundance resulted from a combination of abundance shifts of individual species and changes in the composition of the dependent plant flora across sites. Other variables that were also important were the surface area of the branch and the abundance of non-vascular epiphytes. Holo-epiphyte richness was positively correlated to bryophyte cover and negatively to lichen cover.

The work here presented highlighted the importance and the paucity of research on mechanically dependent plants in Honduras and discussed the contribution of hurricane-related incidents to the diversity and composition of the dependent plant flora in CNP.

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Project supervisor Dr. Daniel L. Kelly (center), research assistant Nicholas Hill (left) and principle investigator Sven P. Batke (right). Image was taken by Vishnu Mohanan, 2013.

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List of Abbreviations

A = accidental epiphyte

AIC = Akaike Information Criterion

ANOVA = Analysis of Variance

BA = Buenos Aires

BC = Base Camp

BIC = Bayesian Information Criterion

BM = Natural History Museum London

C = climber

CA = Cantiles

CAL = Canopy Access Limited

CNP = Cusuco National Park

COL = Climatological Observer's Link

DEM = Digital Elevation Model

ED = hurricane Eye Diameter

EVSS = Exposure Vulnerability Site Score

EXPOS = a model for estimating topographic exposure to wind

GIS = Geographic Information System

GU = Guanales

H = holo-epiphyte

ha = hectare

HURDAT = Hurricane Best Track Data

HURRECON = Hurricane Reconstruction

Ip = Transformation index

IV = indicator value

K = Kew

kPa = kilopascal

kt = knots

LiDAR = Light Detection and Ranging

LM = Linear Model

LMM = Linear Mixed Model

MID = Morisita index of dispersal

ML = Maximum Likelihood

NMS = Non-metric Multidimensional Scaling

NOAA = National Oceanic Atmospheric Administration

NV = nomadic vine

oEVSS = observed EVSS (expressed as COL)

P = parasite

Ph = primary hemi-epiphyte

REML = Restricted Maximum Likelihood Estimation

RH = relative humidity

S = strangler

T = temperature

TCD = Trinity College Dublin

TEFH = Cyril Hardy Nelson Sutherland Herbarium

TOPEX = Topographic Exposure

UC = University of California

VIF = Variance Inflation Factor

VPD = Vapor Pressure Deficit

Chapter 1

1.0. Introduction

Mechanically dependent plants (Kelly 1985) such as holo- and hemi-epiphytes, stranglers, nomadic vines, climbers and hemi-parasites (i.e. mistletoes) are among the most characteristic features of tropical rain forests (Richards 1996). Classification of mechanically dependent plants has been based on ecological parameters, the plant-host relationship, the species' growth habit, microclimatic canopy conditions, levels of resource availability and the species' adaptability to different substrata (Benzing 1990).

Holo-epiphytes are the 'true' epiphytes among mechanically dependent plants, which spend all of their life-cycle on a host tree (i.e. phorophyte). They are not parasitic nor do they extract nutrients or minerals directly from their host, but merely use the host for mechanical support (Kress 1986). In contrast, hemi-epiphytes differ from holo-epiphytes in that they have contact to the ground at some point(s) during their life-cycle. Originally the term hemi-epiphyte was applied only to primary hemi-epiphytes (Schimper 1888, Schimper 1898), but was later more widely used to accommodate secondary hemi-epiphytes. Primary hemi-epiphytes germinate on the tree and grow downwards, subsequently seeking contact to the ground, whereas secondary hemi-epiphytes germinate on the ground, climb up and lose their stem connection to the soil. Most recent authors have argued that because some secondary hemi-epiphytes regain connection to the soil at different points during their life-cycle, they do not fit well within the concept of an epiphyte (Zotz 2013a). Thus secondary hemi-epiphytes have recently been grouped into nomadic vines, as they more closely resemble the ecology of a nomadic vine (Moffett 2000). Nomadic vines do not require a terrestrial life cycle phase and are characterized by losing and regaining their connection to the ground, in contrast to true vines and lianas (Moffett 2000). It is important to note that mechanically dependent plants have a high plasticity and that the life-form categories often integrate. For example, the aroid *Philodendron lacerum* (Jacq.) Schott has been classed into four different categories by the same author (Kelly 1985).

Stranglers have been classed into hemi-epiphytes as the individual spends the early part of its life as an epiphyte and subsequently sends down roots to the

soil. However, they differ from primary hemi-epiphytes and nomadic vines in that they outlive their host tree by becoming freestanding, structurally-independent trees. Competitive behaviour for resources between the strangler and the host tree, together with mechanical constrictions of the host's vascular system, generally results in the death of the host tree (Richards 1996). Hemi-parasites (i.e. mistletoes) differ in their ecology from all previously mentioned life-forms in that they are parasitic on the host's xylem, but are simultaneously capable of photosynthesizing. Parasitized hosts often lose limbs or die in the case of heavy infestations (Press and Phoenix 2005, Glatzel and Geils 2008).

In many botanical surveys, mechanically dependent plants contribute substantially to the floristic diversity of a forest (Gentry and Dodson 1987a, Ibisch et al. 1996); it has been reported that a single tree can hold as many as 126 morphospecies [= 1% of the entire vascular flora of Costa Rica; (Schuettpelz and Trapnell 2006)]. Global estimates for mechanically dependent life-forms are somewhat scarce and satisfactory estimates are only available for holo- and hemi-epiphytes and climbers. Holo- and hemi-epiphytes (hemi-epiphytes in the strict sense, excluding nomadic vines) account for 9% of global vascular plant diversity (Zotz 2013b), compared to climbers which represent 2.5% (Gallagher and Leishman 2012). No global estimates exist for stranglers and hemi-parasites. Of the 4000 estimated species of parasitic angiosperms (global quotient of Orobanchaceae = 1%) (Nickrent et al. 1998), only a small proportion is estimated to be hemi-parasitic. Hemi-parasitic mistletoes belong to only a couple of families [e.g. Loranthaceae = approximately 900 species (all life-forms); Santalaceae = approximately 400 species (all life-forms)] (Benzing 1990). This is also true for stranglers, as they are mostly represented by species from the genus *Ficus* [Moraceae; a genus of approximately 1100 species] (Zotz 2013b).

The high diversity of mechanically dependent plants has primarily been associated with the availability of water and high temperatures (Gentry and Dodson 1987b, Benzing 1990), resulting mostly [but see Zotz (2005)] in a higher importance of dependent plants (specifically epiphytes) in lower latitudes (Zotz and Bader 2009, Durigon and Waechter 2011). Thus, tropical forests

have been described as dependent-plant diversity hotspots. For example, Gentry and Dodson (1987a) assessed the contribution of the dependent flora in lowland tropical forests in the world and found that the combined number of holo- and hemi-epiphytes ranged between 0.2-63% of the total plant diversity. Climbers on the other hand contributed between 10-34% to the total plant diversity. Similar estimates were reported for holo- and hemi-epiphytes from Chiapas in Mexico (Wolf and Flamenco-S. 2003) and for lianas from Panama (Schnitzer and Carson 2000).

Studies in tropical forests in Central and South America have reported a remarkably high diversity of dependent life-forms (Nadkarni 1984, Gentry and Dodson 1987a, Gentry and Dodson 1987b, Ibisch et al. 1996, Kreft et al. 2004, Küper et al. 2004, Lüttge 2007, Larrea and Werner 2010, Cascante-Marín and Nivia-Ruíz 2013). For example, records from local floras and checklists have revealed that in some Central American countries, holo- and hemi-epiphytes *sensu lato* (including nomadic vines) contributed up to 27.4% to the total flora (Cascante-Marín and Nivia-Ruíz 2013). In other parts of the world such as Asia and Africa, the dependent flora is often less rich (Madison 1977, Johansson 1989). However, Turner (1994) did a taxonomic account of the Flora of Singapore and found that epiphytes *sensu lato* accounted for 13% of the total vascular flora. Similar high numbers have been reported for lianas in China (Cai et al. 2009) and Borneo (Putz and Chai 1987). Thus, holo- and hemi-epiphyte estimates from tropical regions often exceed the world estimate of 9%.

The great variability in the number of dependent plants recorded between regions is most likely the product of past and present geological, climatic and bio-geographical events (Gentry 1982, Benzing 1987, 1990, Graham 2011). Additionally, the inconsistent botanical cover across localities is also an important reason. In Central America, for example, most research on the dependent flora has been conducted in Southern Central American countries - Panama and Costa Rica (Nadkarni and Matelson 1992, Patino et al. 1999, Laube and Zotz 2006, Marín et al. 2008, Zotz and Schultz 2008, Cascante-Marín et al. 2009, Caceres et al. 2011, Caceres et al. 2013), with less focus on Northern Central American regions such as Nicaragua (Atwood 1984), Belize

(Catling 1997), El Salvador (Méndez et al. 2010), Guatemala (Catling and Lefkovitch 1989, Nesheim and Økland 2007) and Honduras (Decker et al. 2011). The only Northern Central American country that has been covered relatively well is Mexico (Hietz and Hietz-Seifert 1995, Wolf and Konings 2001, Hietz et al. 2002, Wolf 2005, Wolf and Flamenco-S. 2006, Scheffknecht et al. 2010, Vergara-Torres et al. 2010).

Floras and checklists from Central American regions are often lacking or require significant revisions (Table 1.1), which makes it difficult to satisfactorily estimate the total number of mechanically dependent plants for many Central American countries. Honduras in particular has received little specialized botanical attention (Frodin 2001); checklists have been published for seed plants (Nelson 2008) and Pteridophytes (Nelson et al. 1996), but no Flora of Honduras has yet been published. It is still unclear how many mechanically dependent plants Honduras has and, biogeographically, how Honduras compares to other Central American inventories [I am only aware of one published study that specifically addressed epiphytes by Decker et al. (2011)]. The poor representation of surveys on dependent plants in Honduras is most likely the result of the historical political instability of the country, the difficult topography (Graham 2011) and the methodological challenges often associated with canopy science (Sillett and Antoine 2004, Lowman and Schowalter 2012). Access for sampling is often the most ubiquitous challenge to the surveyor, as mechanically dependent plants often grow at great height in the canopy, where conditions for establishment and survival are often more optimal (Benzing 1990, Schnitzer and Bongers 2002, Gianoli et al. 2012).

Table 1.1 Complete and incomplete floras and checklists of different Central American regions.

Region	Title	Type	Completed	Reference
Central America	Flora Mesoamericana (projected: 6 volumes)	Flora	N	TROPICOS.org. Davidse et al.
Guatemala	Flora of Guatemala (Part 1-13)	Flora	Y	Standley et al. (1946-1977)
	Orchids of Guatemala (Part 1-2)	Flora	Y	Ames & Correll (1953-1954)
	Supplement to Orchids of Guatemala and British Honduras	Checklist	Y	Correll (1965)
	Ferns and fern allies of Guatemala (Part 1-3)	Flora	Y	Stolze (1976-1983)
	Orchids of Guatemala and Belize	Flora	Y	Ames & Correll (1985)
	Orchids of Guatemala: a revised checklist	Checklist	Y	Cameron (2000)
Nicaragua	A checklist of the vascular plant of Nicaragua	Checklist	Y	Seymour (1980)
	Flora de Nicaragua (Part 1-3)	Flora	Y	Stevens et al. (2001)
	Flora de Nicaragua (Part 4)	Flora	Y	Gomez et al. (2009)
Honduras	Enumeracion de las plantas de Honduras	Checklist	Y	Molina (1975)
	Hondurensis plantarum vascularium catalogus. Pteridophyta	Checklist	Y	Nelson et al. (1996)
	Catálogo de las plantas vasculares de Honduras	Checklist	Y	Nelson (2008)
Belize	The forests and flora of British Honduras	Checklist	Y	Standley & Record (1936)
	A list of the Monocotyledoneae of Belize	Checklist	Y	Spellman et al. (1975)
	A list of the Dicotyledoneae of Belize	Checklist	Y	Dwyer & Spellman (1981)
	Orchids of Guatemala and Belize	Flora	Y	Oakes & Correll (1985)
	Checklist of the vascular plants of Belize	Checklist	Y	Balick et al. (2000)
	Recent records of pteridophytes from Belize	Checklist	Y	Sutton et al. (2000)
	Additions to the orchid flora of Belize	Checklist	Y	Sayers & Plooy (2003)
	A checklist of the vascular plants of the lowland savannas of Belize	Checklist	N	Goodwin et al. (2013)
El Salvador	Flora salvadoreña: lista preliminar de plantas de El Salvador	Checklist	Y	Calderon & Standley (1941)
	Las Orquídeas de el Salvador (Part 1-2)	Flora	Y	Hamer (1974)
	Las Orquideas de el Salvador (Part 3)	Flora	Y	Hamer (1981)
	An annotated checklist of the Ferns and Lycophytes of El Salvador	Checklist	Y	Monterrosa & Monro (2008)

Table 1.1 (*cont.*)

Region	Title	Type	Completed	Reference
Mexico	Trees and shrubs of Mexico	Flora	Y	Standley (1920-1926)
	Flora taxonomica mexicana	Flora	N	Conzatti (1939-1947)
	Listados florísticos de México	Flora	N	Cabrera (1987)
	The vascular flora of Isla Socorro, Mexico	Checklist	N	Levin & Moran (1989)
	New pteridophyte records for the state of Quintana Roo, Mexico	Checklist	N	Palancios-Rio & Cortes (1990)
	Annotated checklist of the vascular flora of the Chamela Bay region	Checklist	N	Lott (1993)
	The flora of Guadalupe island, Mexico	Flora	N	Moran (1996)
	Flora of the Gran Desierto and Rio Colorado of Northwestern Mexico	Checklist	N	Felger (2000)
	Los géneros de plantas vasculares de la flora de México	Checklist	Y	Villasenor (2004)
	Orchids of Mexico	Flora	Y	Hagsater et al. (2005)
Panama	Flora of Panama Canal Zone	Flora	N(?)	Standley (1928)
	Flora of Panama (Part 1-3)	Checklist	Y	Woodson (1975-1976); D'Arcy (1987)
	The ferns and fern-allies of Costa Rica, Panama, and the Chocó (Part 1)	Checklist	Y	Lellinger (1989)
	Field guide to the orchids of Costa Rica and Panama	Flora	Y	Dressler (1993)
	Catalogo de las Plantas Vasculares de Panama Colombia	Checklist	Y	Correa et al. (2004)
Costa Rica	Flora of Costa Rica (Part 1-4)	Checklist	Y	Standley (1937-39)
	Flora costaricensis	Flora	Y	Burger (1971-?)
	An Introduction to the Pteridophyte Flora of Finca La Selva, Costa Rica	Checklist	N	Grayum & Churchill (1987)
	Flora arborescente de Costa Rica	Flora	Y	Holdridge & Poveda (1975); Zamora (1989, 2011)
	The ferns and fern-allies of Costa Rica, Panama, and the Chocó (Part 1)	Checklist	Y	Lellinger (1989)
	Field guide to the orchids of Costa Rica and Panama	Flora	Y	Dressler (1993)
	Manual de Plantas de Costa Rica (Vol. 1-5)	Checklist	Y	Hammel et al. (2003, 2007)

The mechanical dependency of a plant on a host tree is mostly connected to the structure of the substratum and micro-environmental dynamics of the forest. As the physical structure and the microenvironment changes as one ascends into the canopy, eco-physiological traits allow individuals to exploit different niches. The structural and environmental variability across the canopy allows niche differentiation, which may have resulted in the often observed structured distribution of species and life-forms along individual host trees (Johansson 1974, Johansson 1978). It has repeatedly been established that dependent plants are mostly limited by water and mineral nutrient availability, air temperature, relative humidity and solar radiation within the tree canopy (Laube and Zotz 2003, Cervantes et al. 2005, Winkler et al. 2005, Cach-Pérez et al. 2013). Variation in these is often associated with host properties of particular trees (e.g. canopy architecture, bark texture and the age of the host) (Zotz and Vollrath 2003, Wyse and Burns 2011). The way in which different life-forms respond to these limiting factors mostly depends on the ecology and eco-physiological requirements of individual species. For example, holo-epiphytes are more dependent on the conditions in the canopy compared to hemi-epiphytes and climbers, due to their complete detachment from terrestrial resources. Adaptations such as pseudobulbs, absorbing trichomes and water-tanks thus reflect better adapted canopy life-styles (Benzing 1987, 1990).

Disturbance within the forest canopy (e.g. branch dislodgment and/or defoliation) is likely to cause immediate changes in the forest canopy dynamics (Brokaw and Walker 1991, Nadkarni 2000). As plants are sessile organisms and their establishment site is therefore determined at early stages during ontogeny (Zotz 1997), flexible strategies (e.g. different traits) that enable them to tolerate sudden changes in their environment are expected to be especially advantageous (e.g. the ability to survive long periods of desiccation). Species that are not able to tolerate these changes are predicted to diminish in abundance.

Hurricanes can create dramatic changes in the forest canopy environment (Zimmerman et al. 1994, Everham and Brokaw 1996). Storm damage can result in uprooting of trees, branch damage (e.g. breaking and bending stress),

severe defoliation (Brokaw and Walker 1991) and changes in the forest microclimate. For example, Turton and Siegenthaler (2004) demonstrated that hurricane damage can result in sudden changes in the canopy microclimate by increasing temperature and decreasing relative humidity. Dependent plants can respond to hurricane exposure in two ways: Directly by dislodgment and damage to the photosynthetic tissue and reproductive organs (Mújica et al. 2013) and indirectly, by responding to changes in the canopy structure and microclimate (e.g. increase in irradiation and temperature and decrease in relative humidity). Both response pathways would ultimately result in a shift in the dependent plant community and would differ between canopies that have been differently affected by hurricanes. Indirect effects can also result in a shift of certain dependent life-forms within the canopy to sites that are more suitable.

Little research has been done that assessed the effects of hurricane-related damage on the microclimate and canopy biota (Rodriguez-Robles et al. 1990, Tanner et al. 1991, Loope et al. 1994, Turton and Siegenthaler 2004, Goode and Allen 2008) and it remains to be seen how mechanically dependent plants respond to large, infrequent disturbances (in Honduras and elsewhere). This issue will become of more importance with increased changes in climate (Lugo and Scatena 1992, Hsu et al. 2011) and expected future increases in hurricane impact (Mann and Emanuel 2006).

1.1. Research aims

The overall aims of this thesis were to provide baseline information on the dependent flora of Cusuco National Park (CNP), Honduras and to investigate the diversity and distribution of dependent life-forms across different environmental gradients and along a gradient of past hurricane impact. Specific objectives for each of the data chapters were set out as follows:

The aim of **Chapter 2** was to model the cumulative impact of past hurricane winds in CNP. The aims of the model were to identify the prevailing wind directions and speeds of hurricanes and to compute a high resolution exposure

map that would allow the identification of areas across the park that had been least/most impacted by hurricane winds in the past.

In **Chapter 3**, the model results from Chapter 2 were correlated with microclimate measurements made across individual tree canopies over a 12-month period, to test whether the microclimate varied between trees that had received different degrees of exposure to hurricane winds. It was predicted that different tree species/types differed in their response between hurricane impact sites.

Chapter 4 aimed to provide a first account of the mechanically dependent plants of CNP and to investigate the response of the dependent flora to different environmental variables and along a gradient of past hurricane impact. The objective was to compare the diversity and composition of the dependent flora among plots and trees that had been affected differently by hurricanes, using the model developed in Chapter 2.

The aim of **Chapter 5** was to identify structural and environmental variables that affected the dependent flora across the canopy and between individual branches along a gradient of hurricane impact in CNP.

Chapter 6 aimed to present an overview of the biogeographical contribution and affinity of epiphytes (holo- and hemi-epiphytes) of CNP and of Honduras in relation to other Central American countries.

Chapter 7 provides a general conclusion and synthesis of the thesis. An overview of the main findings and future recommendations are presented.

1.2. Chapter contributions

Each chapter was solely written by the thesis author. Support was provided by other researchers mostly in the form of critical evaluation and comments on draft manuscripts. Table 1.2 summarizes the contributions for each chapter. Additional support was provided by taxonomists, ecologists and statisticians who are not named as co-authors at the beginning of each chapter, but are recognized in the general acknowledgments.

Table 1.2 Data chapter contributions per chapter.

Data chapter contributions	Chapter 2	Chapter 3	Chapter 4	Chapter 5	Chapter 6
Conceived and designed the experiments	SB & DK	SB & DK	SB & DK	SB & DK	SB & DK
Performed the experiments	SB & NH	SB & NH	SB & NH	SB & NH	SB
Analyzed the data	SB	SB	SB	SB	SB
Contributed materials/analysis tools	SB, MJ & DK	SB & DK	SB & DK	SB & DK	SB, CA, & DK
Wrote the paper	SB	SB	SB	SB	SB
Edited the paper	SB, MJ, DK & *R*	SB, DK & *R*	SB & DK	SB & DK	SB, CA, & DK

SB = Sven P. Batke (thesis author)

DK = Daniel L. Kelly (accademic supervisor)

NH = Nicholas Hill (primary fieldwork assistant)

MJ = Merlijn Jocque

CA = Alfredo Cascante-Marín

R = anonymous reviewer

In addition to the chapters presented in this thesis, three additional articles are currently being prepared that incorporate data collected by the authors. One article will assess the role of logging and hurricane damage on forest loss in CNP and will be written in collaboration with Dr. Neil Reid of Queen's University, Belfast. The second article aims to assess the impact of hurricane damage on macro-invertebrates in Bromeliads in CNP (in collaboration with Dr. Merlijn Jocque from the University of New Jersey). The third article will be written in collaboration with Dr. Daniel L. Kelly from Trinity College Dublin, on the vascular plants added to the Honduran flora from CNP. Finally, a short communication was published by the thesis author on a new fern record to Mesoamerica (Batke, S.P. and Hill, N. 2013 - Appendix 3).

1.3. Publication status of the chapters

Chapter 2 (*published*): Batke, S.P., Jocque, M. and Kelly, D.L. (2014). Modelling hurricane exposure and wind speed on a mesoclimate scale: a case study from Cusuco National Park, Honduras. *PlosOne*. e91306.

Chapter 3 (*published*)**:** Batke, S.P. and Kelly, D.L. (2014). Tree damage and microclimate of forest canopies along a hurricane-impact gradient in Cusuco National Park, Honduras. *Journal of Tropical Ecology,* 30, 457-467.

Chapter 4 (*submitted as shortened version and joined with chapter 5*)**:** Batke, S.P., Hill, N. and Kelly, D.L. (2014). Responses of mechanically dependent plant diversity and composition along a gradient of hurricane impact. *Ecology*.

Chapter 5 (*submitted as shortened version and joined with chapter 4*)**:** Batke, S.P., Hill, N. and Kelly, D.L. (2014). Mechanically dependent plans and their response to different branch characteristics along a gradient of hurricane impact. *Ecology.*

In addition, a smaller section of chapter 5 was also published as a separate paper (*accepted*): Batke, S.P., Hill, N., Murphy, B. and Kelly, D.L. (2015). Can air humidity and temperature regimes within cloud forest canopies be predicted from bryophyte and lichen cover? *Ecological Indicators.*

Chapter 6 (*in review*; first decision = minor corrections)**:** Batke, S.P., Cascante, A. and Kelly, D.L. (2015). Epiphytes in Honduras: a biogeographical overview of the vascular epiphyte flora and its floristic affinities to other Central American regions. *Tropical Ecology*.

Chapter 2

Modelling hurricane exposure and wind speed on a mesoclimate scale: a case study from Cusuco NP, Honduras

2.0. Abstract

High energy weather events are often expected to play a substantial role in biotic community dynamics and large scale diversity patterns but their contribution is hard to prove. Currently, observations are limited to the documentation of accidental records after the passing of such events. A more comprehensive approach is synthesising weather events in a location over a long time period, ideally at a high spatial resolution and on a large geographic scale. We provide a detailed overview on how to generate hurricane exposure data at a meso-climate level for a specific region. As a case study we modelled landscape hurricane exposure in Cusuco National Park (CNP), Honduras with a resolution of 50 x 50-m patches.

We calculated actual hurricane exposure vulnerability site scores (EVSS) through the combination of a wind pressure model, an exposure model that can incorporate simple wind dynamics within a 3-dimensional landscape and the integration of historical hurricanes data. The EVSS was calculated as a weighted function of sites exposure, hurricane frequency and maximum wind velocity.

Eleven hurricanes were found to have affected CNP between 1995 and 2010. The highest EVSS's were predicted to be on South and South-East facing sites of the park. Ground validation demonstrated that our model explained 73% of physical tree damage. The South solutions (i.e. the South wind inflow direction) explained most of the observed tree damage (71% of the observed tree damage in the field). Incorporating historical data to the model to calculate actual hurricane exposure values, instead of potential exposure values, increased the model fit by 50%.

2.1. Introduction

The contribution of high energy weather events to community dynamics and large scale diversity patterns both through alterations of the community structure as well as long distance dispersal is often assumed but hard to prove (Peterson 2000). The only information currently available is from studies comparing community structure and diversity before and after the passing of hurricanes [but see Tanner et al. (2014)]. In most cases observations are collected after the unexpected passing of hurricanes (Bellingham et al. 1992), often through long term observation plots (Walker 1991). Such occasional observations have limited general applicability. A more comprehensive approach is synthesising weather events in a location over a long time period, ideally at a high spatial resolution and on a large geographic scale (Xi et al. 2008). This would improve our understanding on how large weather events contribute to community dynamics and diversity patterns. Little such information is available [however see Boose et al. (1994)], but the availability of advanced geographical software, the wealth of detailed weather data and high resolution images of geographic topography provide the means to generate such data (Rossi et al. 2013).

Hurricanes are well defined and relatively predictable weather events, with a well monitored path trajectory. Hurricane storms are dynamic weather fronts that change in size, speed and intensity throughout their life time. These highly organised systems often originate over tropical and subtropical waters, moving westwards with a counter clockwise rotation in the Northern Hemisphere. The compilation of a hurricane exposure map for a particular region, expressing the accumulated impact of past hurricanes, can be calculated through the combination of 1) a wind pressure model, 2) an exposure model that can incorporate simple wind dynamics within a 3-Dimensional landscape and 3) the integration of previous hurricanes during the considered time period.

The wind pressure model is the core of the calculations and predicts how wind speed decays from the centre of the hurricane. In the past 30-40-yrs significant advances in sensing and analytical hurricane hind- and forecasting technology have allowed a more accurate representation and assessment of hurricane

wind models and damage (Harper 2002). Of particular interest was the mathematical representation of the empirical wind-pressure relationship (Holland 1980, 2008, 2010). The relationship between minimum central pressure and maximum surface winds can be used as a basic parametric radial wind profile model, to estimate the wind impact beyond a certain radius from the hurricane centre (Vickery et al. 2000). The wind pressure model generates wind speeds for all points in a region for a passing hurricane.

The actual impact of the winds in those locations also depends on the topography of the landscape. A landscape can be broken down into localities differently affected by passing large weather events - largely determining the local mesoclimate. Topographic exposure has been defined as a geomorphometric feature that is characterised by its degree of protection by the surrounding landscape (Mark 1975, Mikita and Klimanek 2010). The geomorphometry of a landscape can be assessed by means of digital elevation models (DEM) in the GIS (Geographical Information System) environment. The level of topographic exposure is often very difficult to model, as wind direction and velocity can change as a function of topographic complexity, vegetation type and local abiotic climate conditions (Ostertag et al. 2005). A basic topographic exposure model (EXPOS) can be used that assesses wind exposure as a simple function of relative height and distance to the surrounding horizon (Boose et al. 1994, Mikita and Klimanek 2010). EXPOS evaluates each point on the DEM as more or less protected or exposed, providing the points fall within the wind shadow cast by points upwind. In other words, the bending inflection angle of the wind is fixed as it passes over the landscape. The degree of inflection angle can also help to categorise areas that are more or less likely to be affected by winds (Boose et al. 1994).

These two core components generate an exposure map, expressing the effective impact of a single hurricane passing through a region. Therefore, integrating individual hurricane exposure scores into a single map will give a more relevant ecological and biogeographical image of the affected region. The practical application of EXPOS, combined with exposure models such as TOPEX (Topographic Exposure) and HURRECON (Hurricane Reconstruction)

has most frequently been explored in the forestry sector (Boose et al. 1994, Boose et al. 2004, Lanquaye-Opoku and Mitchell 2005), where wind damage assessments are a common tool in timber and conservation management. For example, wind damage can be a driving force in landscape-level community patterns by affecting vegetation dynamics (Hanewinkel et al. 2011), when storm forces exceed the resistance of trees to either breakage or overturning (Zimmerman et al. 1995, Pietre et al. 2009). Applications of these models and risk assessments are commonly performed at single sites and until now direct comparisons of large and infrequent disturbances between sites are rare. This is largely due to the difficult to quantify effect of topography amongst sites (Peterson 2000). An integrative model that allows for a high resolution comparison of cumulative site vulnerability over large areas would therefore be most valuable in forest management, as it can help to assess individual ecosystem (e.g. tree, stand level) responses to different exposure levels over time (Xi et al. 2008).

Additionally, geographical site information on cumulative hurricane impacts would contribute significantly to the biogeography of diversity. This will be important as a good understanding of the influence of large storms on terrestrial ecosystems and diversity patterns will grow in importance with changing climates. For example, recent modelling of tropical storm incidences shows that over the last 30-yrs the frequency of tropical storms remained largely the same but that intensity increased (Emanuel 2005, IPCC 2013). Such an increased intensity of extreme weather events could reinforce the interaction between climate and community dynamics and could further influence the distribution of organisms and diversity patterns (Censky et al. 1998).

To contribute to the understanding of community structure, dynamics and diversity patterns in relation to high energy weather events, we compose a cumulative hurricane exposure map, synthesising the effect of hurricanes in the last 15-yrs, on a high spatial resolution (50 × 50 m) for Cusuco National Park in Honduras. We therefore adjusted an existing model (Boose et al. 1994, Boose et al. 2004) to predict the impact of hurricane winds on a mesoclimate level in a landscape. Our new model adds a cumulative impact factor of historical

hurricanes. The aimed outputs of the model were i) prevailing wind directions, ii) the wind speeds of historical hurricanes in a specific area and iii) a high resolution exposure map highlighting past hurricane impact.

To evaluate the model we correlated model predictions with field observations of tree damage and an onsite evaluation of topographic exposure in Cusuco National Park. Physical tree damage is almost exclusively the result of high intensity weather (Mattheck and Breloer 1994) and should be a good indicator of hurricane exposure.

2.2. Material and Methods

2.2.1. Study area

Cusuco National Park (CNP), at 15°32'31"N and 88°15'49"W is located in the Departmentos Santa Barbara and Cortes in NW Honduras in close proximity to the border with Guatemala (Figure 2.1). The park was established in 1959 and is currently designated as a National Park under Decr. 87-87 and the IUCN category II. Cusuco's vegetation consists of semi-arid and moist tropical mountain pine forest dominated by *Pinus maximinoi* H.E. Moore and *Pinus tecunumanii* F. Schwerdtf. ex Eguiluz & J.P. Perry, and moist broadleaved forest, with dwarf forest at higher elevations (Hartshorn 1983). The topography of CNP is mountainous with a minimum elevation of 600 m asl. and a maximum elevation of 2242 m asl. within the core-zone boundary. The Park has one visitor centre (Base Camp; 15°29'15"N and 88°12'42"W), the villages St. Tomas (15°33'43"N and 88°18'01"W) and Buenos Aires (15°29'59"N and 88°10'45"W) and four camping sites (Cantiles; 15°30'45"N and 88°14'22"W, Cortecito; 15°31' 15"N and 88°17'20"W, Danto; 15°31'43"N and 88°16'36"W and Guanales; 15°28'55"N and 88°13'48"W).

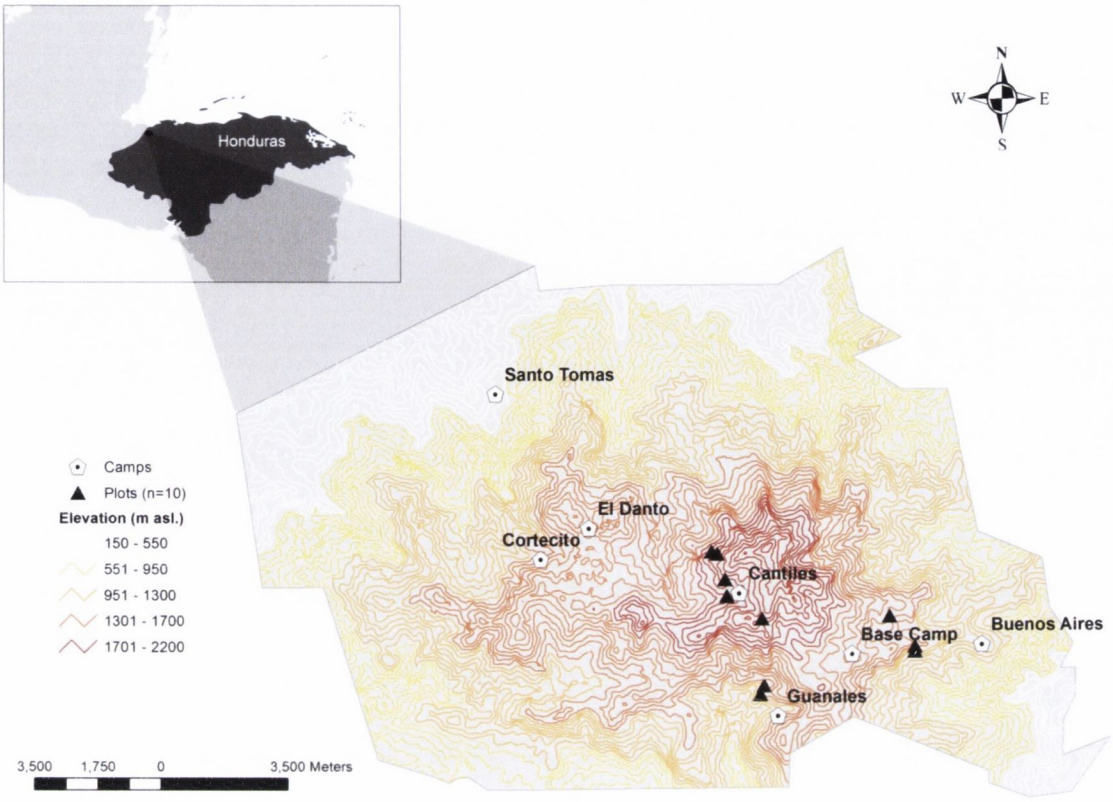


Figure 2.1 The delineation of the Cusuco National Park (CNP) boundary and situation in Honduras (15°32'31"N and 88°15'49"W). Camp sites are illustrated on a 50 m resolution contour map, as well as plot locations of the 2012 and 2013 summer season.

2.2.2. Modelling hurricane wind fields

For this study hurricane Best Track Data (HURDAT) were obtained from the National Oceanic and Atmospheric Administration (NOAA) (NOAA 2012). The data file contained hurricane track data from 1851 to 2010. We used hurricanes that intersected within a 480 km buffer from CNP and were recorded between 1995 and 2010. The 480 km buffer was chosen because it averages a typical hurricane width (NOAA 1999). However, track data for stronger hurricanes (Category > 3) outside the buffer were independently assessed for their potential inclusion under larger hurricane radii assumptions (i.e. > 480 km). We used hurricanes from the last 15-yrs as data on the 6-hourly centre location

(latitude and longitude) and intensities (maximum surface wind speeds and minimal central pressure) were available for these. The x/y-track data were plotted using ArcGIS 10 (ESRI 2011).

The model presented here to calculate the hurricane wind field was based on a basic pressure-wind model as often used in hurricane studies (Harper 2002, Boose et al. 2004):

$$v_m = a\Delta p^{x} \qquad \text{(Eq. 2.1)}$$

where a and x are empirical constants, v_m is the maximum wind speed, Δp is the pressure drop from a defined external pressure to the central pressure ($p_n - p_c$). In this study the external pressure was defined as p_n = 1015 for the western North Pacific and p_n = 1010 for the North Atlantic (Holland 2008). The constant x has often a typical value of approximately 0.7 for near surface winds (Blanchard and Hsu 2005) and was computed as follows (Holland 2008):

$$x = 0.6\left(1 - \frac{\Delta p}{215}\right) \qquad \text{(Eq. 2.2)}$$

Although V_m was available from the data set for each hurricane, V_m was recalculated by the authors using an adjusted pressure-wind model. This was done to test model performance. The model took the following equation (Holland 2008):

$$V_m = \left(\frac{b_S}{pe}\Delta p\right)^{0.5} \qquad \text{(Eq. 2.3)}$$

where p is air density, e the base of the natural logarithm and b_s is a function of the hurricane eye latitude and current pressure deficit, calculated as follows:

$$b_s = -4.4*10^{-5}\Delta p^2 + 0.01\Delta p + 0.03\frac{\delta p_c}{\delta t} - 0.014\sigma + 0.15v_t^x + 1.0$$

(Eq. 2.4)

where p_c is the observed central pressure and $\frac{\delta p_c}{\delta t}$ is the intensity change over time (hPa h^{-1}).

To describe the wind speed intensity and the size of the hurricane, wind speed V_m (at the eye-wall) and the radii of maximum winds R_{max} were computed (Harper 2002, Holland 2008, Wang and Rosowsky 2012). In order to calculate a wind gradient from the hurricane centre to the peripheral zone of each hurricane, the hurricane eye-diameter (*ED*) was calculated as:

$$ED = 46.29Exp(-0.0153Z + 0.0166\sigma) \quad \text{(Eq. 2.5)}$$

where σ is the absolute value of latitude and Z is the observed wind speed. The eye-diameter was then used to calculate the radial tangential wind speed beyond R_{max}, V_r as follows:

$$V_r = V_m\left(\frac{R_{\max}}{r}\right)^x \quad \text{(Eq. 2.6)}$$

where r is the distance and R_{max} is the radius of maximum wind speed calculated as follows:

$$R_{\max} = \left(\frac{ED}{2}\right) + 8 \quad \text{(Eq. 2.7)}$$

The wind gradient was calculated around the hurricane centre in 15 km intervals (i.e. 15, 30, 45,... km). In ArcGIS multiple ring buffers were created using the buffer wizard tool. The buffers were based on the wind strength attributes and the fixed distance intervals. In the next step, all hurricane buffers that intersected with the boundary of CNP were extracted to identify hurricane tracking positions of the intersecting hurricanes. The selected tracking positions

were finally used to calculate wind velocity based on the specific distances from each tracking point (that is the hurricane centre) to the centre of CNP (Figure 2.2).

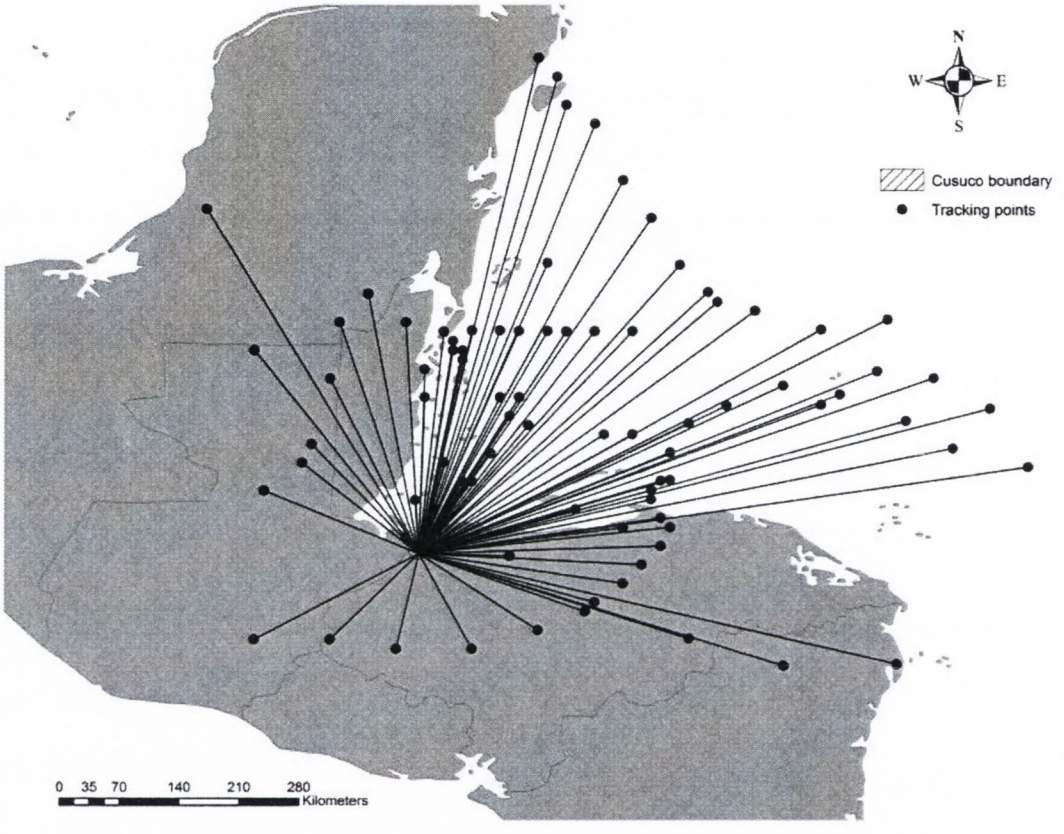


Figure 2.2 The distance from every selected tracking point to the centre of CNP was calculated using the ArcGIS extension 'Spider'.

Wind direction for each hurricane was calculated by finding the interior spherical angle between the hurricane centre and CNP, multiplied by the radius of the Earth as follows:

$$\Delta\theta = RadiusEarth * 2\arcsin\left(\sqrt{\left(\sin^2\left(\frac{\Delta\varnothing}{2}\right) + \cos\varnothing_s \cos\varnothing_f \sin^2\left(\frac{\Delta\lambda}{2}\right)\right)}\right) \quad \text{(Eq. 2.8)}$$

where $\Delta\theta$ is the interior spherical angle, *RadiusEarth* was approximately 6370.97 nkm, $\Delta\varnothing$ is *latitude1* – *latitude2*, $\varnothing_s$ is *latitude1*, $\varnothing_f$ is *latitude2* and $\Delta\lambda$ is *longitude1* – *longitude2*. By assuming a simplified 25 degree tangential inflow angle for hurricanes (Boose et al. 1994, NOAA 2012) the wind direction was estimated in degrees for every hurricane.

The adjusted pressure-wind model (equation 2.5) did not perform as expected. The maximum wind was underestimated by approximately 46%, following comparison with the National Oceanic and Atmospheric Administration (NOAA) data base. As a result, wind velocity at CNP was recalculated using the NOAA V_{max} values instead.

2.2.3. Hurricane Exposure Vulnerability Site Score (EVSS)

A digital elevation model (DEM) of CNP was created using ArcGIS 10 and ArcScene 10 (ESRI 2011). The DEM was based on a 50 m contour-profile map provided by Operation Wallacea (http://opwall.com/) in 2011. DEM's represent a digital and continuous raster surface image of a terrain that can be used to visualize and perform spatial analytical model processes. The DEM was derived using the Topo To Raster tool in ArcGIS. In addition, topographic exposure was modelled using the shade topography tool (hill shade) (Mikita and Klimanek 2010). The tool parameters were set individually for the horizontal angle to eight cardinal points (N, NE, E, SE, S, SW, W and NW) and a vertical angle of 5°, 20° and 45°. The three different inflow angles were chosen because they are most likely to reflect the upper (45°), lower (5°) and observed (20°) extremes for hurricane winds (Boose et al. 1994).

Based on the results from the DEM and the hurricane modelling, an exposure vulnerability site score (EVSS) was designated to areas based on a) the exposure score, b) hurricane frequency and c) wind velocity. The total EVSS was calculated as follows:

$$EVSS = \sum Ef\nu_{\max} \qquad \text{(Eq. 2.9)}$$

In this formula *E* is the exposure score (i.e. the weighted number of exposed and unexposed patches from the GIS raster fields) classed into five discrete categories: 1 = < 45, 2 = 46-90, 3 = 91-135, 4 = 136-180 and 5 = 181-225, *f* the

hurricane frequency over 15-yrs (1995-2010) and v_{max} the maximum wind velocity calculated for each hurricane at CNP. The value v_{max} was classed into three categories following the Saffir-Hurricane index (1 kt = 0.514 m/s) that is 1 = < 20-34 kt (tropical depression), 2 = 35-63 kt (tropical storm) and 3 = > 63 kt (hurricane). The final EVSS's for each cardinal aspect was the weighted sum of the exposure score, the hurricane frequency and the maximum wind velocity. The final EVSS's score were then used as an indicator score for cumulative historical hurricane damage.

2.2.4. Model evaluation

To test how well the exposure model performed, the scores derived from the DEM (that is EVSS) were validated on the ground using an adapted Climatological Observer's Link (COL) and visual tree assessments (Chapman 2000). COL is based on the observer's subjective interpretation of the degree of shelter attributed to a location (scores 0-9). The COL scores (observed EVSS = oEVSS) were correlated with physical tree damage observed within the plots. Damage within each tree was assessed using rope access methods for the upper canopy. Each branch on the tree was assessed for signs of storm damage and an overall damage score was computed based on signs of uprooting, bending or breakage. The oEVSS and branch damage scores were then compared to the model-derived EVSS's using regression analysis. Two models were tested. In model one the oEVSS and the observed branch damage was validated against the EVSS model results. Model two, on the other hand, used the model exposure scores only. This was done to test the fit between the simple (exposure only) and more complex (EVSS) model.

Between June and August 2012 and 2013 a total of ten plots were sampled (Figure 2.1). Plots consisted of 150 x 150-m quadrats. The locations of the plots were selected randomly within the predictive categories from the EVSS maps and a contour map of CNP. Elevation of the plots within each site was between 1200 and 2000 metres. The minimum distance between plots was 50 m. Plots were selected to compare high (EVSS 4-5) and low (EVSS 1-2) exposure sites for model validation at three locations, namely Base Camp (BC), Cantiles (CA) and Guanales (GU). Within these model restrictions, plots were selected based

on the presence of two tree types (angiosperm and *Pinus* sp.) to facilitate comparison of physical damage to trees between plots (see Chapter 3).

The model was developed using Microsoft Excel 2010 (Microsoft Office Professional Plus 2010), ArcGIS 10 (ESRI 2011) and R [R Development Core Team 2012 version 2.14.0 (R Developing Core Team 2011)]. Significance testing between different EVSS's and model performance was assessed using Analysis of Variance (ANOVA) and Linear Modelling (LM).

2.3. Results

Of the 27 hurricanes that were selected only eleven hurricane wind fields impacted CNP and were included in the modelling (Table 2.1; Figure 2.3). Moreover, the vortex-shape of the hurricane wind field changed with each hurricane, as calculated by the model. For example, hurricane 'Mitch' (1998) was one of the strongest hurricanes observed, with a maximum sustained wind speed of 156.42 kt and an estimated wind speed of approximately 55 kt at 318.47 km from the 'eye' (Figure 2.4). In addition, as suggested by the wind-pressure model, wind speed was negatively correlated with air pressure (R^2 = 0.86, $P < 0.001$).

Most hurricane winds that struck CNP were relatively weak with a mean wind speed of 22.35 kt; hurricanes after landfall showed a strong reduction in strength with distance from the centre. The strongest hurricane was 'Wilma' (2005) with a cumulative mean sustained wind speed of 132.02 kt and a maximum sustained wind of 63.5 kt at CNP. On the other hand hurricane Katrina (1999) had only a cumulative mean sustained wind speed of 26.07 kt and a maximum sustained wind of 8.88 kt at CNP (Table 2.1).

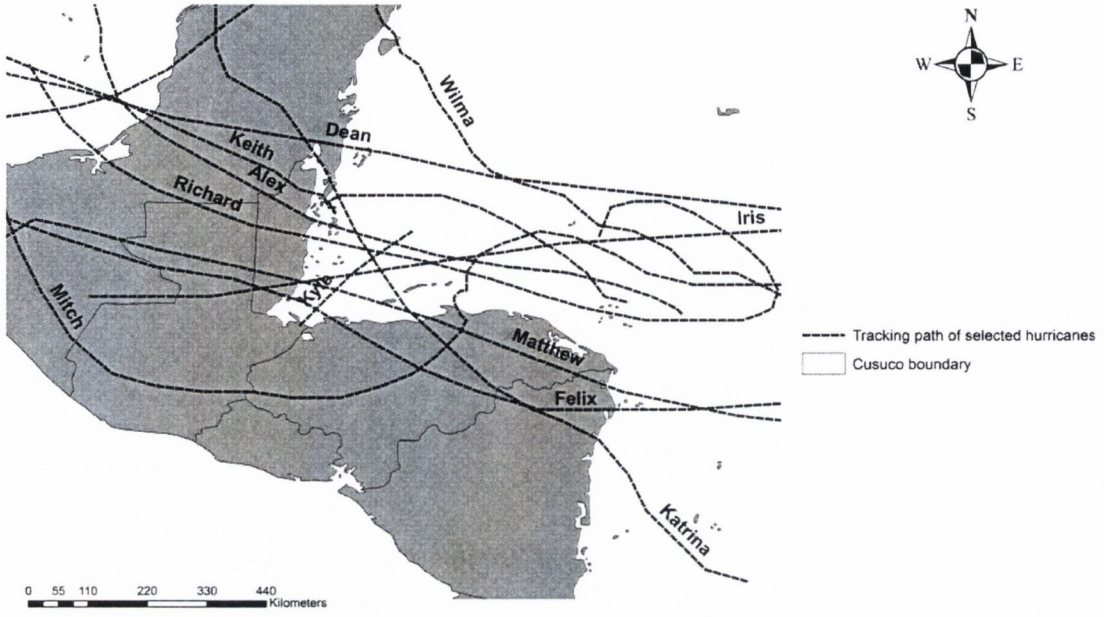


Figure 2.3 The eleven hurricane pathways that were used to calculate the EVSS's for CNP.

Table 2.1 The mean sustained hurricane wind speed in knots (kt) as taken from NOAA (2012), mean distances in kilometre (km) from selected tracking-points to CNP and the modelled mean, minimum and maximum wind speeds at CNP are listed.

Names	Mean sustained winds (kt)	Mean distance to Cusuco (km)	Mean(min./max.) winds at Cusuco (kt)
Alex	56.48	241.99	15.17(14.02/15.77)
Dean	126.00	474.15	37.45(17.29/53.02)
Felix	52.76	266.37	15.11(7.92/32.53)
Iris	106.45	268.29	31.55(16.7/50.47)
Katrina	26.07	196.46	8.60(8.31/8.88)
Keith	77.90	284.02	21.25(8.12/35.82)
Kyle	35.63	104.05	18.68(13.20/28.29)
Matthew	36.21	172.34	12.91(10.65/15.88)
Mitch	89.92	318.47	26.08(9.40/48.85)
Richard	68.65	233.73	18.84(9.91/25.77)
Wilma	132.02	539.82	41.66(26.49/63.50)
Total	**808.08**	**3099.7**	**247.28(142.01/378.78)**
Mean	**73.46**	**281.79**	**22.48(12.91/34.43)**
StD.	**36.57**	**126.53**	**10.53(5.61/17.66)**

Wind direction, assuming a 25° inflow angle, changed between hurricanes and hourly hurricane eye positions (Table 2.2). South and South-East winds were most commonly observed, whereas north winds rarely occurred. The most

northerly winds at CNP came from hurricane 'Mitch' (1998), which circled CNP from the South, then along the West site of CNP, then to the North. On the other hand, hurricane 'Wilma' (2005), for example, varied less in wind direction (Table 2.2).

Table 2.2 Mean wind direction from hourly hurricane centre location towards CNP (NOAA 2012).

	Mean (min./max.) wind direction (°)				
Names	0h	6h	12h	18h	**Mean**
Alex	151.0(-/-)	96.8(-/-)		196.2.1(-/-)	**148.0**(96.8/196.2)
Dean	165.5(-/-)	175.0(-/-)		109.2(72.4/146.0)	**139.7**(72.4/175.0)
Felix	192.3(112.3/272.2)	287.5(-/-)	248.7(241.0/256.4)	191.9(126.5/257.3)	**221.9**(112.3/287.5)
Iris	209.9(-/-)	109.7(-/-)	160.4(-/-)	187.9(-/-)	**167.0**(109.7/209.9)
Katrina	200.4(-/-)	197.6(-/-)			**199.0**(197.6/200.4)
Keith	173.7(144.9/191.1)	164.3(98.6/193.8)	163.8(193.5/192.4)	188.5(183.7/192.7)	**171.3**(93.5/193.8)
Kyle	205.9(-/-)	211.8(-/-)	217.7(-/-)	165.4(131.8/199.0)	**193.2**(131.8/217.7)
Matthew		197.1(-/-)	211.1(-/-)	111.4(-/-)	**172.2**(111.4/211.1)
Mitch	179.0(16.8/293.4)	208.5(132.6/298.1)	163.7(29.7/284.0)	169.5(26.0/288.4)	**180.9**(16.8/298.1)
Richard	155.3(-/-)	104.4(-/-)	143.1(-/-)	199.4(-/-)	**149.1**(94.7/199.4)
Wilma	154.9(147.5/161.8)	150.7(136.5/162.0)	153.8(143.4/165.2)	155.8(150.8/165.0)	**153.6**(136.5/165.2)

2.3.1. Exposure vulnerability at CNP

Modelling topographic exposure at CNP, using different inflection angles (5°, 20° and 45°), yielded different site-exposure distribution curves (Figure 2.5). At a 5° (A) inflow angle the curve took a sigmoidal distribution, with the majority of sites not being exposed. At an angle of 20° (B) and 45° (C) however, the difference of exposure between exposed and unexposed sites was more normally distributed. Therefore, site exposure increased with an increasing inflection angle. With regards to modelled hurricane wind speed and direction, the strongest maximum winds were estimated to have occurred at the South-East (63.5 kt) side of the park, followed by the South (53 kt), North-East (48.6 kt), North-West (47.9 kt), West (33.6 kt), South-West (32.5 kt), East (18.1 kt) and North (13.8 kt).

The EVSS's were calculated using hurricane frequency, maximum wind speed and exposure scores (equation 2.9). The most vulnerable sites, that is with the highest EVSS's, were bare mountain crests, whereas sheltered valley-basins had lower EVSS's. However, EVSS's did not directly change with elevation, but were more a combined response to protection from direct wind influence and

elevation. Average EVSS's for the whole region considered, varied significantly between cardinal directions ($F_{9,14}$ = 1.754, P < 0.001) but not between inflow angles ($F_{2,21}$ = 0.08, P < 0.05). The South and South-East facing sites at CNP had the highest EVSS's (P < 0.001), followed by the North-West and North-East facing sites (P < 0.05).

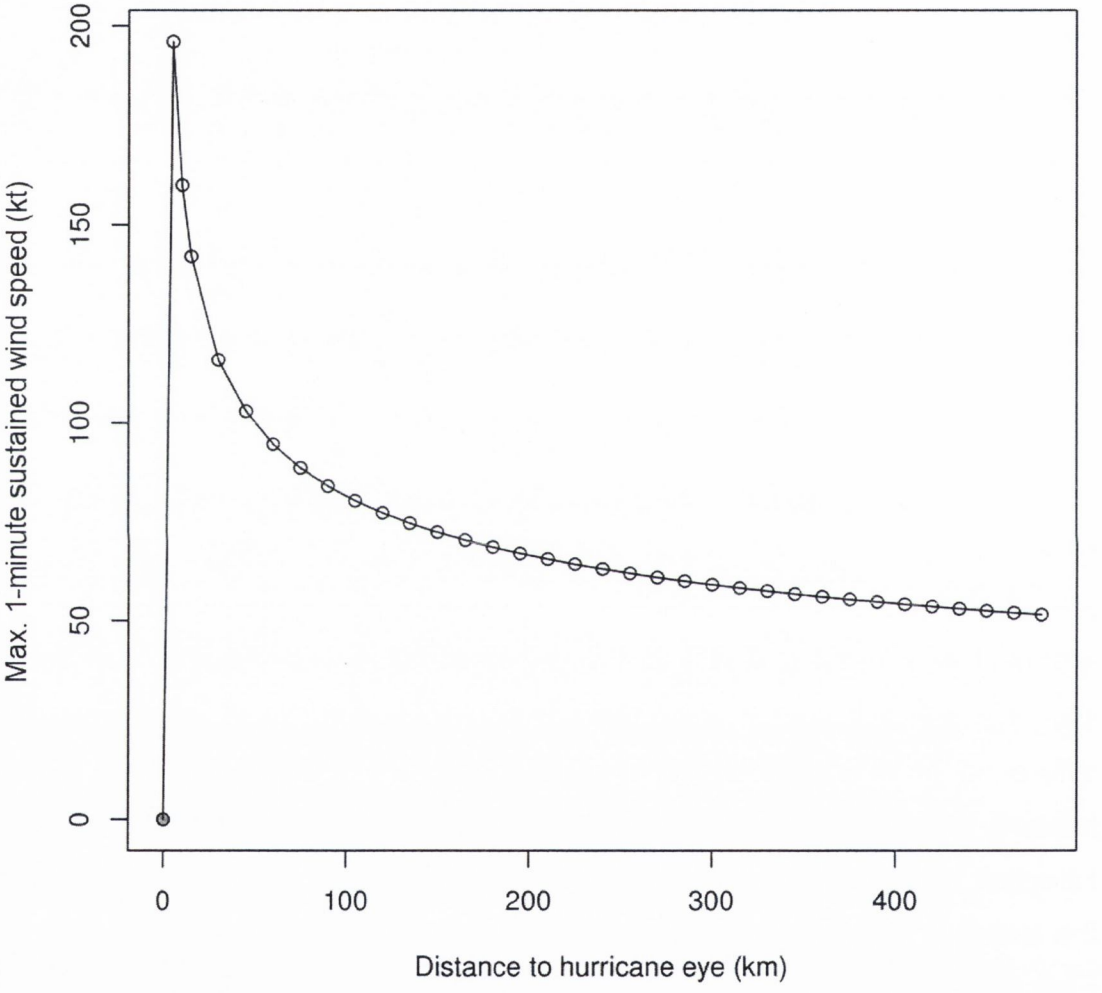


Figure 2.4 Example of vortex shape of hurricane gradient wind field, modelled for Hurricane Mitch (1998).

Because the different inflow angles did not affect the overall EVSS's, the final EVSS maps were derived from a 20° inflow angle (Boose et al. 1994). Figure 2.6 presents four maps (A-D) from the four different wind inflow directions that had the highest observed EVSS scores. It needs to be noted, however, that the

vulnerability map scores between the different maps were adjusted to aid visualisation. For example, Figures 2.6A and 2.6B had EVSS's in the range between 23-34, whereas Figures 2.6C and 2.6D had much lower EVSS's, in the range between 5-7 (Figure 2.6).

Mostly high vulnerability was observed on CNP sites North-West from Guanales and South-East from Base-Camp and Buenos Aires (South and South-East inflow direction). On the other hand, sites with low EVSS's under a South and South-East inflow wind direction, were to be found in the north-west of the Park, in the vicinity of Santo Tomas and Cortecito (Figure 2.6 A-D).

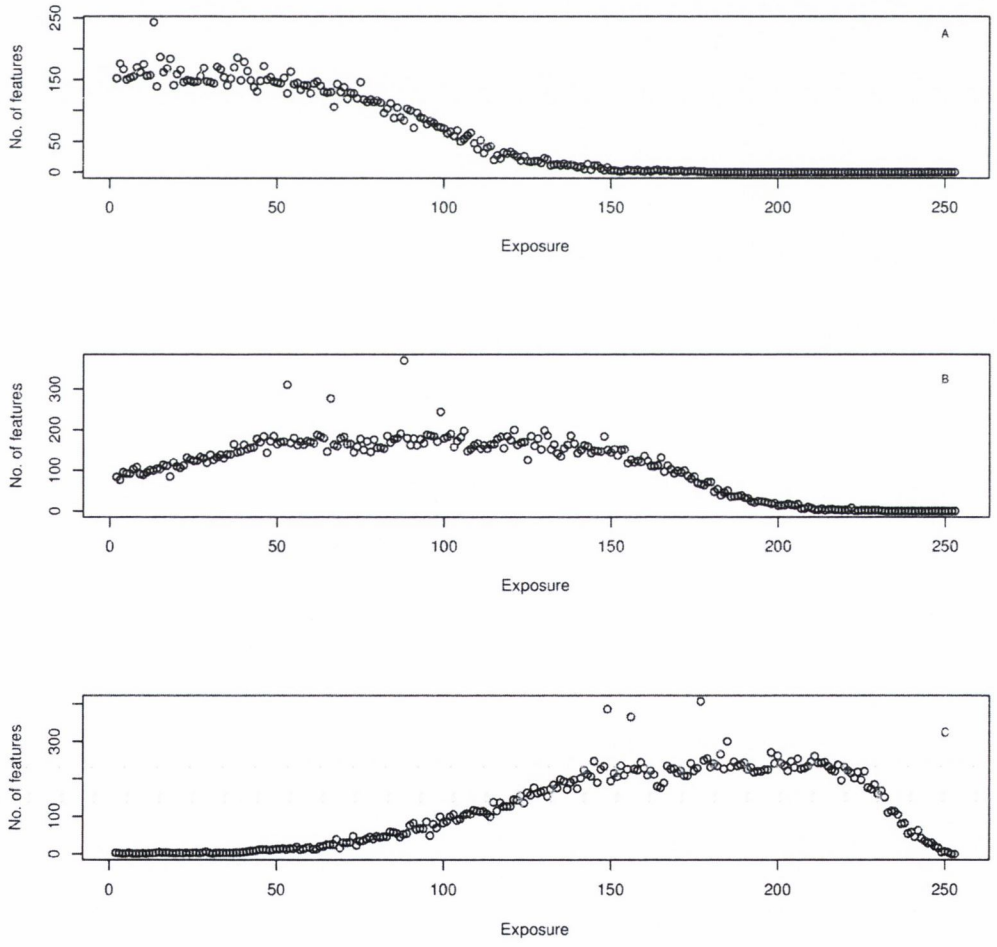


Figure 2.5 Exposure distributions under three different inflow angles, that is 5° (A), 20° (B) and 45° (C). An exposure value of 0 indicates sheltered conditions, whereas higher values indicated an increase in exposure. The number of different features refers to the number of 50 x 50-m squares on the DEM.

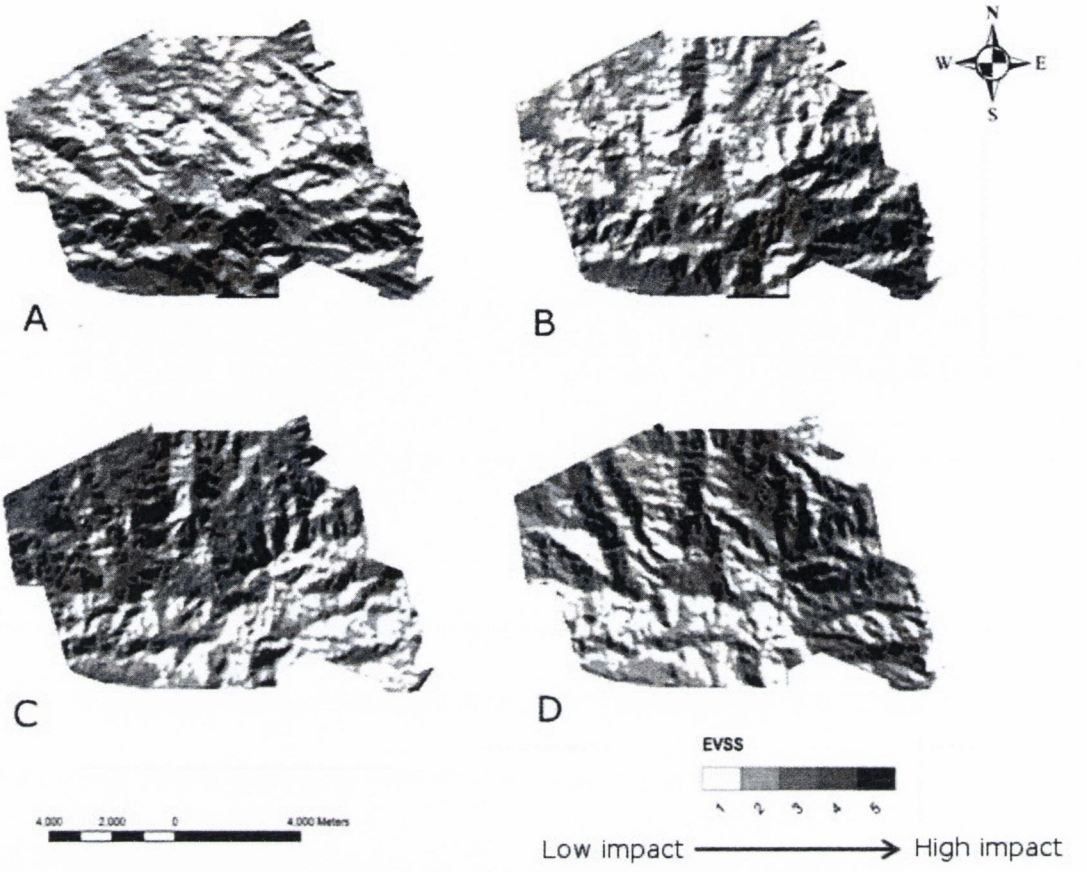


Figure 2.6 Exposure vulnerability site score (EVSS) maps based on equation 2.9, assuming an inflow angle of 20°. An EVSS of one indicates low site vulnerability and a high score high vulnerability. Note that only the wind inflow direction from the South (A), South-East (B), North-West (C) and North-East (D) are shown. EVSS's map scores correspond to a range of 28-34 (A), 23-32 (B), 5-7 (C) and 5-7 (D). The continues score ranges were converted to an EVSS index between 1-5.

2.3.2. Model evaluation

As expected, branch damage on individual trees varied between different model solutions (X^2 = 112.4, P < 0.01) and had a strong positive correlation with the plot oEVSS (Table 2.3). Physical tree damage had a model fit of 73% when all model solutiones were combined in the anlayis (P < 0.05). The more complex model (model 1), which included the frequency and wind speed of all hurricanes explained more of the variation in the data than model two (model 2 was purely based on topography). The South and South-East model solutions explained

most of the observed tree damage on the ground (Table 2.3). All other model solutions were non-significant following Akaike Information Criterion and likelihood analysis ($P > 0.05$).

Table 2.3 Best fit linear model results assessing regression fit of generated exposure vulnerability site score (EVSS) from the South and South East with observed exposure vulnerability site score (oEVSS) and branch damage in two models: purely based on topography (model 2) and topography including frequency and actual wind speed (model 1). The total fit for all model solutions are also presented. The best statistical model was chosen using Akaike Information Criterion (AIC).

Model	Treatment	Std. Error	t-value	Adj. R^2	P-value
Branch damage ~ oEVSS		0.02	4.86	0.82	0.01
Total	All solutions	0.16	na	0.73	0.03
Model 1					
oEVSS ~ EVSS_South + EVSS_SouthEast	South	0.86	4.60	0.90	0.02
	South East	0.84	-2.83	0.90	0.07
Branch damage ~ EVSS_South	South	0.05	3.68	0.71	0.02
Branch damage ~ EVSS_SouthEast	South East	0.06	2.43	0.50	0.07
Model 2					
oEVSS ~ Exposure_South + Exposure_SouthEast	South	<0.01	0.21	0.40	0.84
	South East	<0.01	-4.00	0.40	<0.01
Branch damage ~ Exposure_South	South	<0.01	-0.49	-0.03	0.63
Branch damage ~ Exposure_SouthEast	South East	<0.01	-3.41	0.27	<0.01

2.4. Discussion

We generated a high spatial resolution (50 × 50-m) hurricane exposure map for Cusuco National Park that explained up to 73% of the observed tree damage on the ground. We modeled actual hurricane exposure values, based on data from the last 15-yrs. Actual hurricane exposure values differ from potential hurricane exposure values (Boose et al. 1994) in that they synthesise the impact of all hurricane events over a specified period. Potential hurricane exposure values present the maximal hypothetical exposure to hurricane winds from a certain direction calculated purely on topographic parameters such as slope, orientation and elevation. We compared the model fit of both the exposure values alone and the values from the complete model (EVSS) to explain physical tree damage. Our model predicted that for exposure values alone, the South-East solution performed significantly better than the South

solution (Table 2.3), the total solution explaining 40% (Adj. R^2 = 0.4) of the observed variance. However, when the ground data were tested as a function of EVSS, the South solution performed significantly better (Adj. R^2 = 0.9) (Table 2.3). Our results showed that the calculation of actual values, instead of exposure values only, can change the relevance of wind direction and so increase the model fit by 50%.

Only eleven hurricanes affected CNP in the last 15-yrs, and thus only eleven events were incorporated in our model. Moreover, many only reached tropical storm strength. Despite the low number and in many cases relatively low strength of hurricanes, the model still efficiently explained the majority of hurricane related field observations at CNP. Most probably the calculation of actual hurricane exposure values from the last 15-yrs allowed the identification of major hurricane pathways along the reserve. As repetitive wind damage can result in forest stand adaptations to disturbance (e.g. changes in species composition and forest structure), particularly when the frequency and intensity of the disturbances are high (Everham and Brokaw 1996), it can be predicted that forest communities will respond along this impact gradient. The long-term recovery of forests after wind disturbance has been shown to vary greatly between stands and species and is often very slow (Zimmerman et al. 1994). In a review on forest damage and recovery after catastrophic winds it was pointed out that forest recovery can be divided into four components: namely regrowth, recruitment, release or repression (Everham and Brokaw 1996). Each component is controlled by biotic and abiotic site conditions and the frequency and severity of disturbance events. As these components vary considerably between species, repetitive wind damage will alter the recovery dynamics by impeding a fast recovery for some species and/or stands.

We found that 71% of the variation in physical tree damage was explained by our South-model solution, with the majority of branches on standing trees showing signs of breakage and bending stress. These results are similar to other studies in the Caribbean (Brokaw and Walker 1991), which found that the main direct effects by hurricanes were defoliation, uprooting and snapping; whereas indirect effects included ultraviolet damage to understory juveniles (You and Petty 1991), alteration in species recruitment, the forest microclimate

and species composition (Frangi and Lugo 1991). In the case of CNP the damage inflicted on trees by severe winds was significantly affected by the exposure of the trees (Reilly 1991), but more importantly, by the frequency and the maximum speed of hurricane winds that occurred at these sites. Wind damage to stands can be variable (Foster and Boose 1992) and often are controlled by the vegetation height, composition and specific site characteristics (Xi et al. 2008). For example, it has been shown that damage probability increases with tree diameter and tree species. Trees such as *Pinus taeda* L. showed the highest risk probability followed by *Liquidambar styraciflua* L., *Quercus* spp. and other broadleaves (Xi et al. 2008). Similar results were found elsewhere (Zimmerman et al. 1994). Given that significant stretches of forest in CNP are dominated by *Pinus* spp., this could potentially further alter forest dynamics along the gradient of hurricane impact. It would therefore be desirable to include structural and floristic vegetation data of the affected region (Foster and Boose 1992, Xi et al. 2008). However, in the case of CNP this is currently restricted by the limited account and comprehensive knowledge of the forest's vegetation.

Our model's mathematical representation of a hurricane was simplified, and we briefly would like to point out a couple of possible points for amelioration of the model. Firstly it was assumed that the storms were circular in section. Hurricanes, however, are dynamic weather fronts that constantly change in size, shape, direction and strength (Boose et al. 1994). Also, the model did not account for precipitation changes or strong convective cells. Soil erosion due to high precipitation (Perotto-Baldiviezo et al. 2004) could increase the overall effect hurricane winds have on the local vegetation by increasing the risk of uprooting (Philpott et al. 2008). As CNP lies within a very mountainous region [80% of the slopes in Honduras exceed 20%, (Smith 1997)], increased soil erosion after severe rain becomes very likely (Perotto-Baldiviezo et al. 2004). Evidence of this was seen in Honduras and Nicaragua following hurricane Mitch in 1998, when intense rain triggered widespread landslides and flooding (Perotto-Baldiviezo et al. 2004). The risk probability of landslides was strongly correlated with slope and land cover type (Perotto-Baldiviezo et al. 2004). Therefore our predicted EVSSs' are likely to be conservative, as the inclusion of

vegetation and soil erosion probability could increase the overall vulnerability to tree damage (e.g. weakening of the rooting substrate and increased mechanical stress).

In conclusion, the model used here is a powerful tool to identify major hurricane pathways in the landscape and provides the means to evaluate the historical impact of hurricanes on ecosystems, environmental stability and diversity patterns of organisms. The model provides readily interpretable data in the form of discrete hurricane exposure values, wind speed direction and intensity that can easily be applied to test hypotheses.

Chapter 3

Tree damage and microclimate of forest canopies along a hurricane-impact gradient in Cusuco National Park, Honduras

3.0. Abstract

Past studies of large, infrequent wind disturbances have shown that topographical, biological and meteorological factors interact to create complex damage patterns to forest ecosystems. However, the extent to which some of these factors change the forest microclimate along a vertical forest profile is poorly known. In a previous study, we correlated tree damage with a hurricane model that estimated past hurricane impacts within Cusuco National Park, Honduras over a 15-y period. Here we use the model to compare physical tree damage among different species in ten 150 × 150-m plots and to correlate modelled exposure from hurricanes to microclimate measurements along the vertical canopy over a 12-month period. It was found that past hurricane impacts could still be detected long after the events. Different tree species showed different levels of wind damage. Most branch damage was observed on conifers (*Pinus* spp.), followed by angiosperm species. Vapour pressure deficit increased with height in the canopy and with increased disturbance level. A linear model explained 83% of the total variance in vapour pressure deficit, with 67% attributed to monthly fluctuation, 15% to elevation, 12% to historical hurricane damage and 6% to height in the canopy.

3.1. Introduction

The damage that large infrequent disturbance events, such as hurricanes and cyclones, can cause to forest systems has been widely discussed (Everham and Brokaw 1996). The focus has been on abiotic factors that influence patterns of damage (Martin and Ogden 2006) and effects on the composition and structure of forest vegetation (Zimmerman et al. 1994). However, little information is available on the micro-environmental effects that large storm events have on forest canopies (Turton and Siegenthaler 2004, Turton 2013).

The structural impact of infrequent high-energy weather events depends on the properties of regional and local stands (Martin and Ogden 2006), the geographical environment and the frequency, strength, duration, severity and size of the disturbance event (Everham and Brokaw 1996, Sturtevant et al. 2014). For example, topographic sheltering can reduce the local impact on forest trees, while their vulnerability to wind damage can increase on exposed sites such as ridge tops (Brokaw and Grear 1991). Repetitive wind damage may result in either stand adaptations to wind damage (de Gouvenain and Silander 2003) or increased vulnerability to additional disturbances through changing stand physiognomy (Uriarte et al. 2004). The scale of the impact is highly variable and can extend from mass uprooting of trees, to branch damage (e.g. breakage, bending stress and wounds), to defoliation of the canopy.

The effects that these structural changes have on the micro-environment of the forest are also closely linked to the degree of disturbance. The changes in light environment along with the resulting increase in temperature maxima and decrease in humidity are particularly striking (Turton and Siegenthaler 2004). Consequently, change in the forest micro-environment can have wide-reaching implications for the forest stand and associated biota (Benzing 1990, Cach-Pérez et al. 2013). Little is known about the recovery of forest micro-environment and even less about microclimatic changes along the vertical forest profile after disturbance (Turton and Siegenthaler 2004).

To assess how the forest micro-environment changed following long-term exposure to hurricane winds in Cusuco National Park, Honduras, we developed a model that allowed us to identify areas that have been least/most impacted by hurricanes over a 15-y period (1995-2010) (Chapter 2). The model was verified on the ground using tree damage as a proxy for wind impact (Chapter 2). As the forest canopy will be structurally altered as a result of past wind disturbances, it can be hypothesised that the forest microclimate will differ along a gradient of hurricane exposure.

To investigate this, we tested the correlation between predicted hurricane exposure and the local microclimate within individual trees (expressed as VPD). It was predicted that VPD will increase in tree canopies that are found in high-

exposure sites, as they are likely to be more affected by hurricane winds. As the response to wind damage is predicted to change among tree species, we also expected to find differences in VPD among them.

3.2. Methods

3.2.1. Study site

Cusuco National Park (CNP) is located in the Departments of Santa Barbara and Cortés in north-west Honduras (15°32'31"N, 88°15'49"W; Figure 3.1). Cusuco is situated within a mountainous, high-rainfall region. Maximum elevation is 2242 m asl, with a mean monthly precipitation of 211 mm and an annual precipitation of approximately 2500 mm (Baker 1994). The wet season in CNP is between May-November and is followed by a shorter dry season between December-April (Harborne et al. 2001). The long-term average probability of hurricanes striking a particular point in Central America is 0.2 hurricanes y^{-1} (Pielke et al. 2003). Honduras falls within a hurricane belt that is estimated to have a 5-10% chance of being hit by a hurricane each year (Pielke et al. 2003) (Figure 3.1). Between 1995 and 2010, 11 hurricanes affected CNP. However, most winds at CNP did not reach hurricane strength, as many of the storms only passed the Park at great distance (Chapter 2).

The forest in CNP consists of a complex mosaic of forest types that is the subject of ongoing study by the Forest Botany team of Operation Wallacea, led by D.L. Kelly over the period 2004-2013 (http://opwall.com/). Mixed broadleaved and pine forests dominate most of the Park; *Liquidambar* (Hamamelidaceae), *Pinus* (Pinaceae) and *Quercus* (Fagaceae) being among the principal genera. The families Melastomataceae, Lauraceae, Rubiaceae and Euphorbiaceae are also well represented. At the highest elevations a well-defined elfin forest is present.

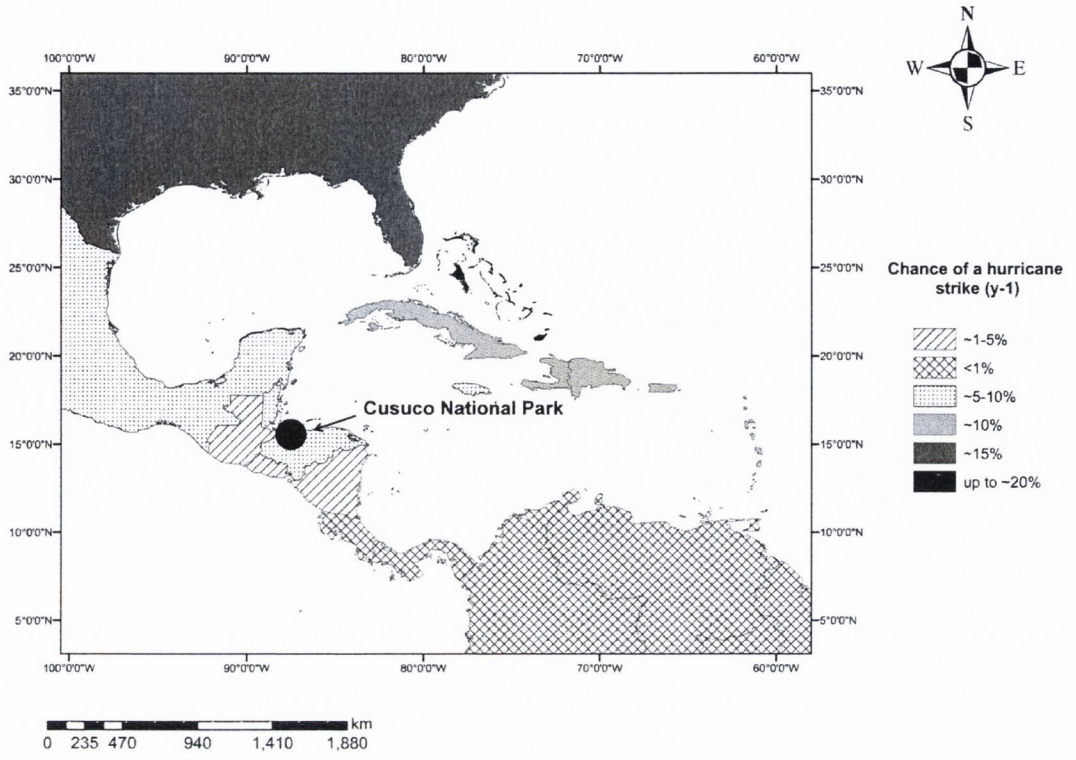


Figure 3.1. Annual likelihood of hurricane activity per country, in the Caribbean. The north-east Bahamas and the coastal region in the Atlantic basin has the highest strike probability, followed by regions such as the Lesser Antilles through the British and U.S. Virgin Islands, southern Haiti, Puerto Rico, Dominican Republic, central Bahamas, the Cayman Islands and western Cuba. Moderate hurricane risk areas (~5%-10%) include countries such as Jamaica, Turks and Caicos Islands, Belize, Honduras and the Yucatan and western Gulf of Mexico. Our study site Cusuco National Park, indicated by a circle, lies within the moderate risk area. Moreover, countries south of 10°N latitude have an annual hurricane risk probability of < 1 %. Data were adapted from Pielke et al. (2003).

3.2.2. Hurricane model

A hurricane model was used to predict the high-energy weather impacts at CNP from 1995 to 2010 (Chapter 2). The model was based on data provided by the National Oceanic and Atmospheric Administration (NOAA) and a digital elevation map (DEM) of CNP. The model predicted hurricane exposure at a high-resolution (50 × 50-m) for eight cardinal model solutions. Each model solution represents the predicted hurricane exposure from different cardinal

wind-inflow directions within CNP. Each 50 × 50-m raster field on the DEM is expressed as an exposure vulnerability site score (EVSS). The scores are between 1 and 5 (low-high exposure) and represent the topographic exposure of each raster field, the hurricane frequency (i.e. number of hurricanes) and the maximum wind velocity calculated for each hurricane. The individual models were assessed following validation on the ground using tree assessment methods and by correlating the exposure scores to the observed tree damage on the ground. Damage on individual trees in CNP was explained best by the correlation of tree damage with the south and south-east model solutions (i.e. exposure to south and south-easterly winds) (Chapter 2).

3.2.3. Plot and tree selection

Between June and August 2012 and 2013 a total of ten plots were sampled. The locations of the plots were chosen using the results from the hurricane model and a contour map of CNP and randomly selected as described in Chapter 2. The size of the plots was 150 × 150-m, and minimum distance between plots was 50 m. The plots had an altitudinal average ± SD of 1595 ± 269 m asl. The original aim was to sample three large *Pinus* sp. and three large angiosperm trees (*Quercus* sp. or *Liquidambar styraciflua* L.) within each of the ten plots. However, because of anthropogenic forest disturbance and scarcity of *Pinus* sp. and *L. styraciflua* at higher elevations this was not always possible. As a result, other angiosperm species that had similar architectural properties to *Quercus* sp. (i.e. a decurrent canopy) were randomly selected and surveyed. On sites where *Pinus* spp. were absent, additional angiosperm species were investigated. Compared to the decurrent canopy and evergreen ecology of most angiosperms investigated, *L. styraciflua* had an excurrent canopy and was deciduous.

Branch damage on each tree was assessed using rope climbing methods (Chapter 2). Trees were selected based on (1) tree diameter at breast height (> 150 cm) and (2) safe climbing-accessibility, thereby excluding all toxic species (e.g. *Toxicodendron*) as well as ant-trees (e.g. *Cecropia*). Tree species were identified at Kew (K), the Natural History Museum (BM), Trinity College Dublin (TCD) and the Cyril Hardy Nelson Sutherland Herbarium (TEFH). Only large

trees were surveyed as they are more susceptible to wind damage (Foster and Boose 1992) and they most fully represent the vertical range in microclimate regimes (Shaw 2004) and epiphyte diversity.

To assess how observed branch damage differed among tree species and types, individual trees were divided for the analysis into groups (i.e. bins) based on morphological characteristics and/or genus. This was done for statistical comparison, as the number of some host trees was relatively low. Group one consisted of *Quercus* spp., *L. styraciflua*, conifers (*Pinus maximinoi* H.E. Moore and *P. tecunumanii* F. Schwerdtf. ex Eguiluz & J.P. Perry, two species of similar overall morphology) and other angiosperm species (*Cedrela odorata* L. and *Ilex pallida* Standl., *Dendropanax* aff. *hondurensis* M.J. Cannon & Cannon). Group two consisted of *L. styraciflua*, conifers and other angiosperm species, whereas group three was simply divided into conifers and other angiosperm species.

3.2.4. Climate data

Data loggers (Luscar EL-USB-2) were suspended on two of the six trees within each plot (n = 20). Loggers were placed at three levels within the tree canopy, viz.: lower, middle and upper canopy. The height of each logger depended on the total tree height. Each of the three data loggers was at the same horizontal distance from the bole of the tree (i.e. the inner canopy). Some of the data loggers were paired, in order to assess recording precision. The loggers measured relative humidity and temperature at 10-min or hourly intervals from June 2012 to June 2013.

Autocorrelation in the climate data was tested for using a Durbin-Watson test, which confirmed a first order-autocorrelation (d = 0.598). To compensate for this autocorrelation, we used loglinear models and treated the factor 'Month' as a random variable and 'Plot' and canopy position ('Position') as nested random variables. To avoid multicollinearity between variables in the models (Heikkinen et al. 2006), only the variable with the highest Variance Inflation Factor (VIF) was retained (O'Brien 2007).

3.2.5. Calculating VPD

Transpiration rates, amongst others, are limited externally by VPD and internally by hydraulic conductivity and water potential between the leaves and the soil (i.e. the capacity to transport available water) (Koch et al. 2004). Although there has been much debate on the usefulness of using VPD to explain temporal dynamics in transpiration (Streck 2003, Bacon 2004), it is believed that VPD can be a useful indicator of potential transpiration for many species, particularly when they are closely coupled to the atmosphere (Adelman et al. 2008). VPD is biologically more relevant to many forest organisms than relative humidity (RH) (Rambo and North 2009), because it reflects more closely differences in water stress (Donald 1936). As a result, monthly RH and temperature (T) measurements (n = 386,469) were converted into VPD, using the formula by Murray (1967) as adapted by Bolton (1980).

Sunrise and sunset times for the years 2012 and 2013 were calculated by averaging daily sunrise and sunset data for each month. The data were obtained from Time and Date (www.timeanddate.com). Mean time of sunrise was 05h44 (± 12 min) and 17h52 (± 14 min) for sunset. It was assumed that VPD = 0 when temperature was ≤ 0°C (Rambo and North 2009). Bolton (1980) showed that this assumption for VPD is sufficiently accurate (0.1%) for temperatures between -30°C and 35°C. As a first step, saturation vapour pressure (e_s) was calculated after Bolton (1980) as follows:

$$e_e = 6.112 \times \exp\left(\frac{17.67 \times T}{T + 243.5}\right) \qquad \text{(Eq. 3.1)}$$

where T is the temperature (°C). Because hourly temperature and RH measurements were available, the actual vapour pressure (e_a) and VPD were determined as follows:

$$e_a = e_s(T) \times \frac{RH}{100} \qquad \text{(Eq. 3.2)}$$

and

$$VPD = e_s - e_a \qquad \text{(Eq. 3.3)}$$

The calculated VPD was correlated to the different model solutions, elevation, tree species and data logger position within the canopy, and compared between different plots and months.

3.3. Results

3.3.1. Branch damage

Branch damage differed significantly among different tree groups (Pearson's Chi-square; grouping 1: $X^2 = 106$, $P < 0.01$; grouping 2: $X^2 = 82.8$, $P < 0.01$; grouping 3: $X^2 = 78.4$, $P < 0.001$). Standardized residuals from loglinear models (LLM) showed that most of the difference in observed branch damage between different tree types was among conifers and angiosperms (Table 3.1). Branch damage was significantly higher for *Pinus* trees than for angiosperms, and the latter had significantly higher numbers of undamaged branches (Table 3.1).

Table 3.1 A LLM pairwise residual comparison was made to compare branch damage responses following hurricane perturbation at Cusuco National Park, among different tree groups. Group one consisted of *Quercus* spp., *Liquidambar styraciflua*, conifers (*Pinus maximinoi* and *P. tecunumanii*) and other angiosperm species. Group two consisted of *L. styraciflua*, conifers and other angiosperm species. Group three consisted of conifers and angiosperm species. Comparisons were made among branches that were not damaged (none), had minor damage (minor) and were severely damaged (severe). P-values are given for each comparison. The plus and minus signs indicate the direction (positive or negative) of the comparison.

Tree group	One	One	One	Two	Two	Two	Three	Three	Three
Damage	None	Minor	Severe	None	Minor	Severe	None	Minor	Severe
Other angiosperms	(+)	(-)	(-)	(+)	(-)	(-)	(+)	(-)	(-)
	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Liquidambar	ns	ns	ns	ns	ns	ns			
Pinus (conifer)	(-)	(+)	(+)	(-)	(+)	(+)	(-)	(+)	(+)
	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Quercus	ns	ns	ns						

3.3.2. Vapour Pressure Deficit

Linear mixed models (LMM) with random nested effects were used to identify changes in mean VPD as a function of the eight hurricane exposure solutions, elevation, position in the canopy and different tree species. A Shapiro-Wilks test and visual assessment were used to test for data normality. No further transformation was necessary ($P < 0.05$). VPD was not included as a seasonal (i.e. dry/wet) or diurnal measurement, but merely as a monthly measurement. This was done because 'Month' had the highest VIF. Monthly VPD was strongly correlated with diurnal VPD (Adj. $R^2 = 0.97$, $P < 0.01$) and seasonal VPD (Adj. $R^2 = 0.99$, $P < 0.01$). Moreover, diurnal VPD was strongly correlated to seasonal VPD (Adj. $R^2 = 0.98$, $P < 0.01$).

As a first step, the eight different hurricane exposure solutions, which predicted the hurricane exposure from different wind-inflow directions, were compared using maximum likelihood (ML) ratio tests. The south solution (i.e. exposure to south and south-easterly winds) was the model with the best fit (AIC = 582.07). In a second step, the south solution model was remodelled using different interaction and random-effect combinations to identify the contribution of different nested and random effects on the overall model performance (Table 3.2). Note that the interaction terms (e.g. plot x position) were not included here, as the overall variance did not significantly contribute to the total variance of the models. The best-fit model remained model one (M1a). Here VPD was measured as a function of the south hurricane solution (i.e. best fit solution); elevation as a fixed effect; and plot, canopy position and monthly fluctuation as random nested effects. The final model was re-run using the restricted maximum likelihood estimation (REML) (AIC = 597.3; Table 3.3). Due to the low variance of each random effect (total variance = 0.7%), all random effects were removed from the model and a linear model (LM) was used instead. The fitted LM explained 83% of the total variance, of which 67% was attributed to monthly fluctuation, 15% to elevation, 12% to historical hurricane damage and 6% to canopy position (Table 3.4).

Table 3.2 Assessing VPD in Cusuco National Park, Honduras. Maximum likelihood ratio tests were used to identify how VPD changed in response to elevation, monthly fluctuations, plot location, canopy position (namely lower, middle and upper canopy) and hurricane exposure (i.e. EVSS_S). The tests were run using different interaction and random effect combinations. The model with the lowest AIC and BIC (Bayesian information criterion) was retained (i.e. the best-fit model) and a Chi-squared test was used to test for significance (Pr>Chisq).

Model	Form	df	AIC	BIC	Pr(>Chisq)
M1a	VPD ~ 1 + EVSS_S + Elevation + (1|Plot) + (1|Position) + (1|Month)	7	580.51	609.14	<0.01
M1b	VPD~ 1 + EVSS_S + Elevation * (1 | Plot) * (1 | Position) * (1 | Month) * (1 | Species)	8	582.07	614.78	<0.01
M1c	VPD ~ 1 + EVSS_S + Elevation + (1 | Plot) + (1 | Position) + (1 | Month) + (1 | Species)	8	582.07	614.78	>0.05
M1d	VPD ~ 1 + EVSS_S * (1|Plot) * (1|Month) * (1| Position)	6	591.94	616.47	>0.05
M1e	VPD ~ 1 + EVSS_S + Elevation * (1|Position) * (1|Month)	6	711.68	736.22	>0.05
M1f	VPD ~ 1 + EVSS_S + Elevation * (1|Plot) * (1|Month)	6	743.98	768.52	>0.05
M1g	VPD ~ 1 + EVSS_S + Elevation * (1|Plot) * (1|Month) * (1|Species)	7	745.84	774.47	<0.01
M1h	VPD ~ 1 + EVSS_S + Elevation * (1|Plot) * (1|Position)	6	1225.18	1249.72	>0.05
M1i	VPD ~ 1 + EVSS_S + Elevation * (1|Plot) * (1|Position)* (1|Species)	7	1227.18	1255.81	>0.05
M1j	VPD ~ 1 + EVSS_S + Elevation * (1|Plot) * (1|Species)	6	1256.27	1280.8	>0.05

Table 3.3 The best-fit model that explained most of the variation of VPD in Cusuco National Park, Honduras. The model was rerun using restricted maximum likelihood estimation (REML). The contribution to the model of each random and fixed effect is presented.

Variables	Effects	Variance	SD	Estimate	Error
Month	Random	0.8	0.9		
Plot	Random	0.2	0.4		
Canopy position	Random	0.1	0.4		
Tree species	Random	0	0		
EVSS south	Fixed		0.1	0.1	0.8
Elevation	Fixed		<0.005	-0.002	-3.8

VPD was significantly different among different tree species (df = 435, P < 0.01) and types (df = 435, P < 0.01). The main differences were observed between conifers and angiosperms. Angiosperm trees, with the exception of *L. styraciflua* (t = 6.6, P < 0.01), had significantly lower VPD compared to conifer trees (t = 5.9, P < 0.01). However, as the variation of VPD in the model (i.e. M1a) was not significantly explained by different tree species (Table 3.2), tree species was not analysed further as a variable.

Table 3.4 Summary of the variance from the LM that explained most of the variation in VPD in Cusuco National Park, Honduras. For each contributing variable (i.e. month, elevation, EVSS south and canopy position), the remaining variance (exclusion of individual variables from the model), the difference in variance and the total variance (%) are presented.

Variables	Remaining variance (Adj-R^2)	Difference (Adj-R^2)	Total variance (%)
Total variance	0.83	0.17	100
Month	0.53	0.48	67
Elevation	0.18	0.82	15
EVSS south	0.14	0.86	12
Canopy position	0.07	0.93	6

Micro-environmental canopy conditions (i.e. VPD) differed amongst heights within the canopy, as well as the months in which the results were recorded (Figure 3.2; Table 3.5). Although seasonal and diurnal VPD changes were not included in the overall model, significant differences between mean VPD in the dry and wet seasons were detected ($df = 439$, $F = 15.8$, $P < 0.01$), with the dry season having significantly higher VPD (2.8 ± 1.09 kPa) compared to the wet season (2.4 ± 1.1 kPa). Additionally, a Tukey Honest Significant Differences (TukeyHSD) test showed that VPD changed significantly between night and day ($df = 1$, $F = 29.7$, $P < 0.01$). This difference was consistent throughout the year ($df = 11$, $F = 3040$, $P < 0.01$), with the only non-significant comparisons between months being December/August ($P > 0.05$), May/February ($P > 0.05$) and October/January ($P > 0.05$).

An analysis of variance (ANOVA) with Bonferroni adjustment revealed that VPD varied significantly between different canopy positions ($df = 438$, $F = 17.5$, $P < 0.01$). The lower canopy had significantly lower VPD compared to the middle ($P < 0.01$) and upper canopy ($P < 0.01$). However, the middle canopy did not differ statistically from the upper canopy ($P > 0.05$).

Table 3.5 Mean and standard deviation of changes in VPD in Cusuco National Park, Honduras. The mean, maximum and minimum VPD for each month are given for the lower, middle and upper canopy.

	VPD_{mean}			VPD_{max}			VPD_{min}		
Month	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
January	1.35 ± 0.53	1.75 ± 0 .43	1.82 ± 0.65	6.83 ± 1.66	7.27 ± 0.93	7.38 ± 1.5	0.02 ± 0.06	0.04 ± 0.09	0.03 ± 0.08
February	2.84 ± 0.96	3.53 ± 0.68	3.67 ± 0.99	6.09 ± 1	6.68 ± 0.81	6.69 ± 0.95	0.16 ± 0.19	0.23 ± 0.31	0.27 ± 0.25
March	2.45 ± 0.49	3 ± 0.35	3.11 ± 0.41	6.49 ± 0.53	6.84 ± 0.29	6.94 ± 0.39	0.04 ± 0.09	0.13 ± 0.23	0.06 ± 0.15
April	3.5 ± 0.89	4.19 ± 0.65	4.44 ± 0.78	8.04 ± 1.01	9.11 ± 0.37	9.24 ± 0.79	0.2 ± 0.29	0.25 ± 0.33	0.32 ± 0.3
May	3.07 ± 0.99	3.71 ± 0.82	4.01 ± 0.85	8.62 ± 1.56	9.41 ± 1.61	9.99 ± 1.54	0.28 ± 0.35	0.38 ± 0.39	0.45 ± 0.41
June	2.25 ± 1.03	2.73 ± 1.06	2.88 ± 1.12	5.88 ± 1.66	6.8 ± 1.82	7.15 ± 2.01	0.29 ± 0.34	0.48 ± 0.42	0.45 ± 0.36
July	2.04 ± 0.69	2.45 ± 0.72	2.78 ± 0.83	6.22 ± 1.02	6.91 ± 1.26	7.9 ± 1.62	0.38 ± 0.36	0.55 ± 0.45	0.49 ± 0.38
August	2.23 ± 0.77	2.8 ± 0.74	3.19 ± 1.02	6.71 ± 1.29	7.2 ± 1	7.89 ± 1.37	0.55 ± 0.6	0.76 ± 0.77	0.86 ± 0.94
September	2.29 ± 0.8	2.87 ± 0.65	3.08 ± 0.73	7.29 ± 1.48	7.83 ± 0.94	8.62 ± 1.21	0.41 ± 0.35	0.72 ± 0.37	0.63 ± 0.37
October	1.29 ± 0.62	1.87 ± 0.49	2 ± 0.59	5.6 ± 1.54	7.21 ± 1.1	7.97 ± 1.71	0.09 ± 0.12	0.15 ± 0.23	0.14 ± 0.14
November	0.47 ± 0.29	0.77 ± 0.34	0.8 ± 0.43	5.39 ± 0.64	6.37 ± 0.41	6.52 ± 0.85	0 ± 0	0.03 ± 0.06	0.01 ± 0.04
December	1.92 ± 0.61	2.51 ± 0.45	2.52 ± 0.52	7.66 ± 1.22	8.36 ± 1.24	8.77 ± 0.94	0 ± 0	0.09 ± 0.2	0.02 ± 0.07

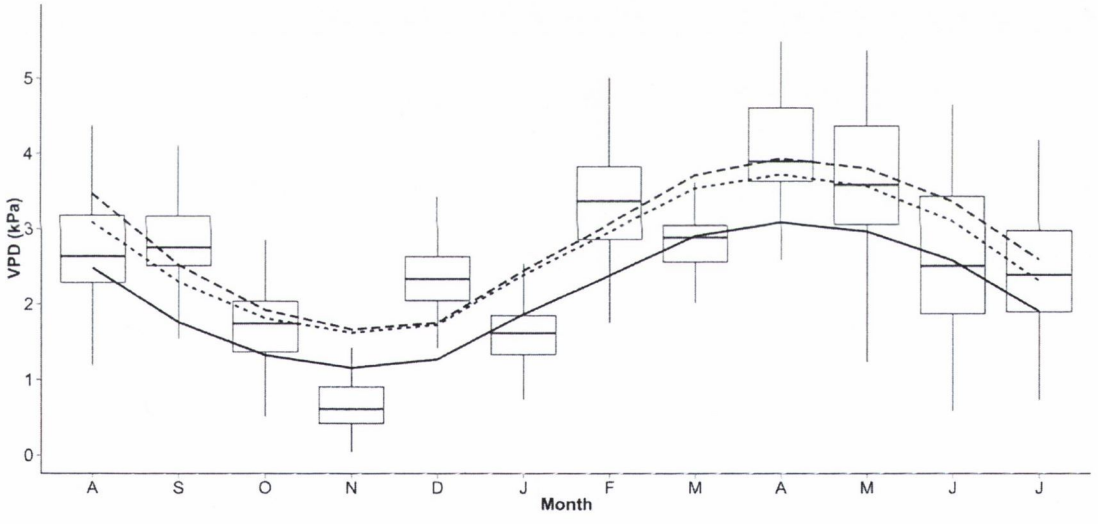


Figure 3.2 Boxplot of mean monthly VPD (kPa) between 2012 and 2013 at Cusuco National Park, Honduras. A linear model (LM) for each canopy position was computed and overlaid. The dashed line represents the modelled mean VPD values for the upper canopy position, the dotted line represents the middle canopy position and the solid line represents lower canopy position.

Additionally, VPD increased with hurricane EVSS (Estimate = 0.28, F = 74.2, R^2 = 0.14, P < 0.01), with the exception of EVSS 4. Differences between exposure levels were detected following pairwise comparisons among EVSSs 1, 3 and 5

(P < 0.01); 2, 3 and 5 (P < 0.01); 3 and 4 (P < 0.01) and 4 and 5 (P < 0.01). Mean VPD increased with height in the canopy and increased hurricane exposure. VPD was significantly lower in canopies that were less likely to be impacted by hurricanes compared to canopies that were more likely to be affected (lower: t = 5.48, P < 0.01; middle: t = 8.04, P < 0.01; upper: t = 9.51, P < 0.01) (Figure 3.3).

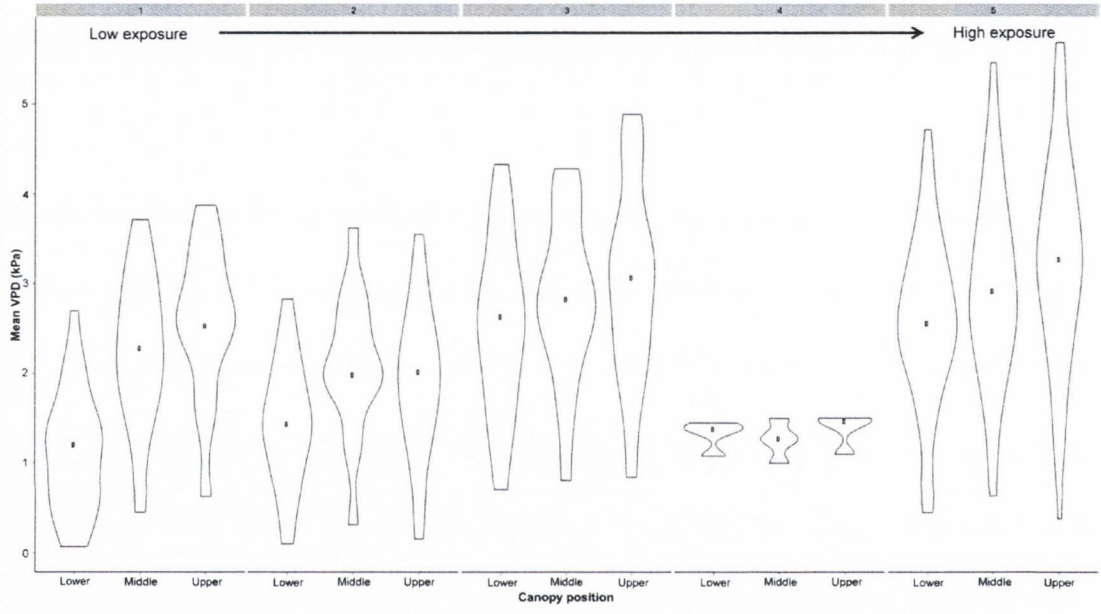


Figure 3.3 Violin plot of mean monthly VPD (kPa) for each canopy position and hurricane exposure site at Cusuco National Park, Honduras. The violin plot is a combination of a boxplot and a kernel density plot, which shows the spread and the probability density of the data. The hurricane exposure sites (EVSS 1 = low impact; EVSS 5 = very high impact) are indicated by the grey boxes at the top of the figure. The black dot symbolizes the median.

3.4. Discussion

The effects of disturbance by hurricane winds depends on the spatial environment of the trees, their proneness to damage, the frequency of hurricane events, and the size and intensity of prior disturbances (Turner et al. 1998, Boose et al. 2001, Xi et al. 2008). For example, Foster & Boose (1992) found that storm damage increases linearly with increasing tree height, making

taller trees more vulnerable to damage. Emergent trees seem to be particularly vulnerable, as they are less sheltered by the surrounding vegetation and therefore experience increased biomechanical stress (de Gouvenain and Silander 2003, Lewis and Bannar-Martin 2011). The difference of tree damage between trees of different size was not very apparent in our study, because most of the investigated trees were similar in height (mean ± SD tree height = 40.4 ± 9.9 m).

Moreover, tree species may differ in their susceptibility to storm events. *Pinus* spp. had much higher levels of branch damage than the angiosperm canopy species. These findings are consistent with other studies (Brokaw and Walker 1991, Foster and Boose 1992). Xi et al. (2008) reported that the probability of tree damage differs between tree species in a Carolina forest. They found that species such as *Pinus taeda* are more susceptible to hurricane damage compared to species such as *Liquidambar styraciflua*, *Quercus* spp. (deciduous) and *Fagus grandifolia*. Although no statistical differences among *L. styraciflua*, *Quercus* spp. and angiosperm division (group one) were detected in our study, the angiosperm species investigated had significantly lower branch damage compared to *Pinus* spp. This is probably because *L. styraciflua* and *Quercus* spp. have a very similar damage-risk, making the detection of differences in damage more difficult (Xi et al. 2008). The difference between angiosperm and conifer trees may be due to the higher wood density observed in many slow-growing hardwood species (Zimmerman et al. 1994), compared to that of the fast-growing and shade-intolerant conifers. In contrast to Xi et al. (2008), Boucher et al. (1990) found that rain-forest trees (i.e. angiosperm-dominated forest) had higher overall tree damage compared to conifer stands, but that angiosperm species had higher survival due to their resprouting abilities. It is possible that other stand attributes such as composition and physiognomy (e.g. canopy closure), rather than differences in wood and tree properties such as density, elasticity and anchorage (Putz et al. 1983, Brokaw and Walker 1991, McCallum et al. 2007) could have caused this observed difference. Although our study did not investigate stand properties, stand composition and tree density within each plot could have influenced the susceptibility of individual trees to wind damage (Rambo and North 2009). For

example, if the variability of forest canopy height is increased, wind flow turbulence is more severe, thereby enhancing damage susceptibility of the whole stand (Martin and Ogden 2006).

Understanding the differences in probability of wind-damage between tree species and forest stands is important as damage affects the vertical, seasonal and diurnal pattern of micro-environmental condition in the canopy. The formation of gaps and the opening of the canopy due to topping of canopies, branch damage and severe defoliation are some mechanisms that can alter the forest micro-environment. Our study found that VPD was affected significantly by seasonal and diurnal cycles, height in the canopy and the modelled impact of hurricanes. However, our model showed that tree species is not an important factor in explaining differences in VPD between trees. The LM explained 83% of the total variance with 67% attributed to monthly fluctuation, 15% to plot elevation, 6% to height in the canopy and 12% to predicted hurricane damage. The decline in VPD with elevation can be attributed to several causes. The air has a lower water-holding capacity at higher elevation (because the temperatures are lower); also, rainfall and cloud occurrence are higher (Richards 1996). This was clearly observed in one of the plots at EVSS level four (Figure 3.3). VPD was significantly reduced at this plot due to its higher elevation (~2020 m asl.) and possibly because of the shorter stand height observed at this plot. The low variability in that plot can be attributed to the recording failure of the logger equipment between November and June. Thus only data for the period between June-August was available for these trees.

Studies that investigate micro-environmental gradients in forest canopies are often limited by incomplete and periodic data records and are often restricted to the lower canopy (Fetcher et al. 1985, Bohlman et al. 1995, Stuntz et al. 2002, Turton and Siegenthaler 2004). Saldaña et al. (2013) investigated micro-environmental differences in the lower part of the canopy (ca. 5-10 m above ground level) between different forest successional stages and found that VPD increased with height in the canopy. Our study investigated the full range of the vertical forest profile over a 12-mo period and found that a clear climate stratification could be observed along this gradient. VPD increased with height

in the canopy, although the upper and middle canopy did not differ statistically in mean VPD; the lower canopy was significantly different from the middle and upper canopy. The vertical gradient in VPD can be attributed to the differences in solar radiation absorption through the canopy profile (Szarzynki and Anhuf 2001). The elevated heat of the air in the upper canopy produces a stable density stratification of cooler denser air in the lower canopy and warmer, lighter air in the upper canopy. The lower canopy is therefore less connected to the atmosphere, reducing the saturation deficit in some instances to approximately 20% compared to the upper canopy (Szarzynki and Anhuf 2001).

The long-lasting effect of hurricanes on the forest microclimate can be substantial and will vary spatially and temporally (Lugo et al. 2000). Our hurricane exposure model for CNP was able to explain 12% of the variation in mean VPD along a gradient of hurricane exposure. This is striking as the last severe hurricanes that impacted Honduras and CNP were hurricane Mitch in 1998 and Wilma in 2005 [Ensor (2009), Chapter 2]. This highlights the importance of past hurricane perturbations on forest stand structure. These effects will diminish over time (Fetcher et al. 1985) and there is some evidence that the recovery rates might vary spatially along the vertical forest profile (King 1986, Weishampel et al. 2007). For example, Weishampel et al. (2007) used LiDAR remote-sensing technology to detect historical hurricane damage following the 1938 hurricane in New England. They reported that the degree of forest damage varied vertically with height in the canopy and tree diversity. This is important, as the difference in damage susceptibility and recovery rate among different tree types and species can further complicate the picture (Bellingham et al. 1992) and the implications are therefore more difficult to predict.

Early studies reported that the effects of site disturbance on the forest microclimate are highly variable along an intensity gradient and with distance from the disturbance site (Davies-Colley et al. 2000, Meyer et al. 2001). Fetcher et al. (1985) compared microclimatic regimes in single tree-fall gaps and clear-fell sites over a 2-y period and found that an increase in VPD and temperature between different sites increased with canopy openness (i.e. disturbance level).

However, they also noted that these differences declined strongly after only 2-yrs, due to regrowth. Our study showed that mean VPD increased on sites that were more impacted by hurricanes at the lower, middle and upper canopy, with great variability among the different canopy positions. Similar results were observed by Turton & Siegenthaler (2004) in a rain forest in Australia after the passing of cyclone 'Rona'. They found that mean VPD was significantly higher compared to pre-disturbance measurements at a canopy height of 10 m; However, post-hurricane VPD did not significantly differ at 20 and 30 m height in the canopy.

In conclusion, the effects that canopy removal (e.g. defoliation and branch damage) and thinning (Rambo and North 2009) can have on the micro-environment after the passing of hurricanes is of great importance to the forest's long-term persistence. de Frenne et al. (2013) recently reported that forest closure minimises the risk to understorey vegetation under climate change scenarios, by reducing ground-layer temperatures and solar radiation and by increasing RH. Our study revealed that cumulative hurricane impacts (i.e. branch damage and raised VPD) can still be measured long after the passing of hurricane storms (Brokaw and Walker 1991, Weaver 2008). Moreover, the degree of structural damage and the resulting alteration in micro-environmental canopy conditions varied along a hurricane exposure gradient and along the vertical forest profile. It remains to be seen how significant these long-term alterations are to the forest and its biota, as there is limited long-term information available on this (baseline forest plot data for CNP go back only to 2003-2004; Cayuela *et al.* 2012).

Chapter 4

Responses of mechanically dependent-plant diversity and composition along a gradient of hurricane impact

4.0. Abstract

The past effects that large disturbance events such as hurricanes can have on the forest canopy and the associated mechanically dependent plant community are dependent on the frequency, intensity and severity of the disturbance events. Here we investigated the effects on canopy dependent plants along a gradient of past hurricane exposure in Cusuco National Park, Honduras. We used modelled hurricane exposure values, which predicted the impact of past hurricanes at high spatial resolution for our study area. The model results were validated, by correlating them to physical tree damage on the ground. The validated model was used to assess dependent plant diversity and community responses along a gradient of hurricane exposure. Tree climbing methods were employed to sample 60 large mature trees for different dependent life-forms. We identified 7094 individuals of dependent plants from 214 different species. We found that diversity was negatively related to past hurricane impact. The life-forms that were strongly affected were holo- and hemi-epiphytes. The dependent plant community response also reflected structural changes in the forest canopy. We were able to explain 44.4% of the community dissimilarity among plots by differences in vapor pressure deficit, elevation, aspect, slope and plot exposure. At the individual tree level, 30% of the community dissimilarity was explained (in no particular order) by differences in host tree (angiosperms versus conifers), canopy openness and hurricane damage. We believe that more emphasis needs to be placed on the effect past disturbance events have on mechanically dependent plant communities, particularly in areas that are prone to catastrophic hurricane perturbations. In addition, as this is one of the first studies on mechanically dependent plants in Honduras, we believe that our data provides valuable baseline information, which can be used to inform local and regional conservation efforts.

4.1. Introduction

Disturbance is an important driver in landscape community ecology and can be summarized as "...any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment" (Pickett and White 1985). Any community has been and is shaped by past and present disturbance events (Smith et al. 2012). Disturbance has mostly been divided into disasters and catastrophes, merely defined by the frequency, severity and intensity of the disturbance event (Begon et al. 2009). Disasters are usually more frequent and therefore result in selection pressure to the affected community. Catastrophes are less frequent and their occurrence is often more detrimental to the community, as they may lack the long-term adaptive ability shown in frequently disturbed communities (Begon et al. 2009). The spatial variation in the frequency and intensity of large disturbance events often results in a vegetation mosaic of different ages and successional classes, with associated alterations in microenvironmental conditions. Therefore, past effects of disturbance can produce gradients of vegetation and environmental conditions (Foster and Boose 1992) that often can be measured long after the passing of such events.

Hurricanes (also called typhoons in the Northwest Pacific or cyclones in the South Pacific and Indian Ocean) are one example of a disturbance event that can have devastating effects to a region. Many ecosystems have been altered structurally and biologically as a result of such large weather events (Brokaw and Walker 1991, van der Maarel and Franklin 2012). For example, in forest systems, hurricane impact can result in tree blow-down, below- and above-ground gap formation, mineral and nutrient leaching and soil erosion (Tanner et al. 1991). Heartsill et al. (2010) demonstrated that aboveground biomass was reduced by 50 percent following a category four hurricane in Puerto Rico. Stem density and tree diversity were also significantly reduced. Although the immediate impact was severe, the forest recovery was rapid and almost returned to pre-hurricane structural conditions after 15-yrs.

In most instances, research on disturbance events such as hurricanes has mainly focused on the immediate effects (catastrophic) of damage but past

effects of disturbances (catastrophes, disasters) have often been neglected (Wagner et al. 2014). In two previous papers (Chapter 2 and 3) we modeled the impact of past hurricanes for Cusuco National Park (CNP), Honduras over a 15-y period and demonstrated that past effects on the forest canopy (expressed as Exposure Vulnerability Site Score – EVSS) and on the canopy microclimate (expressed as vapor pressure deficit – VPD) can be detected long after the passing of hurricane events. We also highlighted that past effects were very important in the long-term development of the forest canopy. As many canopy-dwelling organisms are dependent on the canopy for survival (Sillett and Antoine 2004), it can be predicted that structural and micro-environmental effects of such disturbance events will affect a broad range of forest-dependent organisms. However, the scale at which canopy organisms respond is very difficult to predict and is dependent on the model organisms.

Mechanically dependent plants (Kelly 1985) such as epiphytes, for example, are plants that depend on trees for physical support (Kress 1986). They are closely dependent on the forest structure, environment and composition, and any direct and/or indirect alteration would result in a dependent plant community response (Callaway et al. 2002, Aguirre et al. 2010, Gehrig-Downie et al. 2011). Mechanically dependent plants can be affected by hurricane disturbances in different ways. Direct effects can result in dislodgment or damage to the photosynthetic tissue and/or reproductive parts. Indirect effect may include a shift in the competitive advantages of certain species over others, as a result of damage to the host tree and alteration of the canopy microclimate. The extent to which dependent plants respond will depend on species-specific traits (ecophysiological and morphological) that enable them to tolerate or adapt to these changes (Rees et al. 2001), and to the underlying effects of the changed forest structure (Zimmerman et al. 2014) and composition (Robertson and Platt 2001) following perturbation. For example, dependent plants that have high water use efficiency, a robust photo-protective capacity and a rooting system that enables them to withstand strong winds, are expected to become more prevalent in canopies that have been more frequently damaged by hurricanes (Goode and Allen 2008). This is because high winds can cause tree defoliation and canopy gap formation, which can

lead to an increase in solar radiation and temperature and a resulting decrease in relative humidity (Turton and Siegenthaler 2004).

In Honduras, not much botanical and ecological study of dependent plants has been completed to date (see Chapter 6) (Cascante-Marín and Nivia-Ruíz 2013). Research on dependent plants in Mesoamerica has mostly been conducted in Mexico (Hietz and Hietz-Seifert 1995, Wolf and Flamenco-S. 2003), Costa Rica (Holz and Gradstein 2005, Cardelus et al. 2006, Köhler et al. 2010) and Panama (Laube and Zotz 2006, Poltz and Zotz 2011, Wester et al. 2011), with limited studies from Nicaragua (Atwood 1984), Belize (Bridgewater et al. 2006) and Guatemala (Catling and Lefkovitch 1989). In Honduras, the greatest information on dependent plants available comes almost entirely from general vegetation surveys, which give little or no account of their local abundance, composition and diversity. The first published literature on dependent plants from Honduras was in an extensive account on the flora of Lancetilla Valley near Tela (Standley 1931). Since then only few studies have focused on dependent plants [e.g. Molina (2002 *unpublished*) on Bromeliaceae in a cloud forest in Departamento El Paraiso and Decker (2009 *unpublished*) on epiphyte and bird composition in the Copán region of SW Honduras]. The limited botanical treatment of dependent plants in Honduras may be attributed to the country's geographical location, its difficult topography (Graham 2011), the political instability of surrounding states, the slow pace of economic development (Ruhl 1984) and the methodological challenges often associated with canopy science (Sillett and Antoine 2004, Lowman and Schowalter 2012).

To our knowledge no prior attempt has been made to investigate mechanically dependent plants along the full vertical profile of the forest canopy anywhere in Honduras. We also believe that ours is the first study anywhere to assess dependent plant responses along an impact gradient of past hurricanes. Our aims are i) to provide a first account of mechanically dependent plants (i.e. hemi-epiphytes, nomadic vines, climbers, mistletoes and stranglers) from Cusuco National Park, Honduras, ii) to investigate the response of dependent plant diversity and composition along a gradient of past hurricane impact and iii) to identify species that are indicators of different disturbance levels. We

correlated dependent plant diversity and composition data to a model that predicted past hurricane events at Cusuco National Park (Chapter 2) and to structural and environmental data of the sample area. We predict that dependent plants respond differently along a hurricane exposure gradient and that those vascular plants that are more susceptible to high hurricane impact (i.e. exposure intolerant species) will diminish in more exposed canopies.

4.2. Methodology

4.2.1. Study site

See Chapter 2 and 3 for detail.

4.2.2. Plot and tree selection

Data for this study were collected within ten 150 × 150 m (2.25 ha) plots (see Chapter 2 and 3 for more detail). The six largest trees (three *Pinus* spp. and three angiosperms) within each plot were selected (Zotz and Bader 2011) and subsequently surveyed for all vascular mechanically dependent taxa (see below). *Liquidambar styraciflua* L. was the preferred angiosperm species, followed by oak (*Quercus* spp.) and other angiosperm trees. Atypical and/or noxious tree types were avoided, notably palms, tree-ferns, trees with flaky bark (e.g. *Bursera*), trees with irritant properties (*Toxicodendron*), ant-trees (*Cecropia*) and stranglers (*Ficus* spp.). Data were collected at four different levels of scale: namely, the forest plot, the tree, the branch (see Chapter 5 for more detail) and the dependent plant level. At a plot level, aspect, inclination and exposure (as described in Chapter 2) within each plot were recorded.

4.2.3. Data collection

Tree identification was mostly done in the field. For trees that could not be identified in the field, botanical samples were collected for later identification. For each tree, diameter at breast height was taken at a standard height of 1.3 m or above the top of the buttresses. Tree height was measured using a tape measure, from the top of the tree to the bottom where the trunk met the soil at the highest point. Bole height was measured to the first major branch. The horizontal extent of the canopy was estimated at ground level by measuring

from the centre of the tree in the four cardinal directions (north, west, east and south). Tree surface area was calculated by measuring the length and circumference of each branch and by treating the branch as a cylinder, as described by Batke (2012).

Canopy openness has been widely measured using hemispherical photographs (or fisheye photographs) (Roxburgh and Kelly 1995) and can be defined as "the proportion of the sky hemisphere not obscured by vegetation when viewed from a single point" (Jennings et al. 1999). However, these methods have many disadvantages (Chianucci and Cutini 2012), particular when light-reducing atmospheric conditions such as high fog and cloud cover are frequent, as is the case for CNP. A more basic method is to estimate canopy openness by simple visual assessment along an ordinal scale, as is more frequently used in forest management (Jennings et al. 1999). Adopting this approach, visual estimates were made independently by three individual observers from the bottom of each tree. Openness was estimated from the north side of the tree, using a sighting angle of 75^0 to the top of the tree, with a distance of 5 m from the centre of the tree. 'Closed' was defined as where the cover of the tree canopy was > 80%. 'Intermediate' was defined as where the cover of the tree canopy was > 20% and < 80%, and 'open' was defines as where the cover of the tree canopy was < 20%.

4.2.4. Dependent plant sampling and within-tree data collection

The within-tree data collection was undertaken using modern rope access methods (Aldred 2012). Mechanically dependent plants were divided into the following categories following Zotz (2013a) and Moffett (2000): holo-epiphytes, primary hemi-epiphytes (i.e. they germinated in the canopy and subsequently sent roots down to the soil), nomadic vines (i.e. they germinated on the ground and climb upwards, subsequently losing their stem connection to the soil), climbers (i.e. lianas and vines), hemi-parasitic mistletoes and accidental epiphytes. As little is still known about the ecology of many epiphytic and terrestrial plants within CNP, the terms obligate (i.e. exclusively epiphytic) and facultative epiphyte (i.e. sometimes also terrestrial) were not used. Every branch (and bole) that hosted vascular dependent plants was sampled. New

species to the field collection were collected for subsequent identification and their abundance, life-form and fertility recorded. Branches that were difficult to access, usually when < 35 cm circumference, were cut and lowered to the ground for assessment. For species with a perpendicular growth habit [i.e. compact epiphytes (Kelly 1985)], abundance was measured by counting the total number of individuals per branch (or bole). Species that spread laterally by rhizomes (and where individuals are consequently hard to define) were counted in terms of total occupied area (i.e. length and width of the occupied area) and their abundance was estimated as the number of patches observed per branch. It needs to be noted that our sampling design mainly focused on holo- and hemi-epiphytes, thus climbers and nomadic vines are most likely under sampled.

Specimens that were collected during the fieldwork were identified at the Cyril Hardy Nelson Sutherland Herbarium TEFH (at the National Autonomous University of Honduras), the herbarium at Trinity College Dublin (TCD), the Natural History Museum in London (BM) and the herbarium at Kew Botanic Gardens (K). As Honduras is one of the least botanically studied countries in Central America and still lacks a published Flora, relevant published literature from other Central American countries was consulted. Important sources included Gentry and Vasquez (1993), Maas and Westra (2005), Stevens et al. (2001) [Flora de Nicaragua], Standley and Steyermark (1946) [Flora of Guatemala] and Nelson (2008) [Catálogo de las plantas vasculares de Honduras]. Amongst others Duque (2008), Ames and Correll (1985), Hamer (1988) and Hamer (1981) were consulted for identification of Orchidaceae; Croat (1998), Croat (1997), Croat (1983) and Haigh et al. (2011) for Araceae and Mickel and Atehortúa (1980), Mickel and Smith (2004), Gomez (2009) and Moran (1997) for Pteridophytes.

4.2.5. Hurricane model

As described in Chapter 2 and summarized in Chapter 3, we used past hurricane data to model the impact of hurricanes at Cusuco National Park. In Chapter 2 we correlated different hurricane model solutions to tree damage on the ground. Of the observed tree damage, 71% was explained by our hurricane

south solutions (i.e. south prevailing winds). In Chapter 3, we then correlated our different hurricane solution models to microclimate data that were obtained from data loggers across the vertical forest profile; we found that 12% of our microclimate data (expressed as VPD) was explained by our south hurricane model solution (this being the best fit solution). Moreover, VPD increased with increasing predicted hurricane impact. In the work presented here, we are correlating the different model solutions (expressed as exposure vulnerability site score – EVSS) to diversity and composition data for canopy dependent plants in CNP.

4.2.6. Data analysis

The community analysis at plot and tree level was performed on the whole community data set and was not divided by life-forms [the low number of occurrences in some life-form groups would have yielded unreliable ordinations scores (stress value = > 20)]. Juvenile individuals that could not be identified sufficiently and accidental dependent plants were excluded from the community analysis. Individuals that could not be determined to species rank but represented distinctive, single taxonomic entities were treated as separate species.

Chao 1 and Chao 2 (Chao 1987) non-parametric species estimators were used, as suggested by Wolf et al. (2009), to calculate the overall richness of the samples. Chao 1 uses the number of rare species in the sample to calculate the likelihood that there are more undiscovered species, as follows:

$$S_1 = S_{obs} + \frac{F_1^2}{2F_2} \qquad \text{(Eq. 4.1)}$$

Where S_{obs} is the number of species in the sample, F_1 the number of singletons and F_2 the number of doubletons that occurred in the sample. As the value is only an estimation, the degree of uncertainty (i.e. the variance) needs to be calculated as (Chao 1987):

$$variance(S_1) = F_2\left[\left(\frac{\left(\frac{F_1}{F_2}\right)}{4}\right)^4 + \left(\frac{F_1}{F_2}\right)^3 + \left(\frac{\frac{F_1}{F_2}}{2}\right)^2\right] \qquad \text{(Eq. 4.2)}$$

Additionally, species accumulation curves were calculated using the 'specaccum' function in the 'R-vegan' package (R Developing Core Team 2011). Species were divided into life-forms categories, and curves computed using the 'exact' method. The 'exact' method uses the unconditional standard deviation (i.e. a moment-based estimate) which is based on a species estimate of the survey area (Oksanen et al. 2008).

The analysis of the dependent plant community data was performed separately at a plot and tree level. This was done because the contribution of different environmental factors can change with the scale of the sampling unit investigated (Kent 2012). Non-metric multidimensional scaling (NMS) was used to explore variation in plant community assemblages between plots and trees. NMS has increasingly been used in plant community analysis and is thought to be one of the most robust ordination methods. NMS does not assume linear relationships between species and uses ranked distances to overcome the 'zero-truncation' problem (i.e. the high proportion of uncommon and rare species in most ecological datasets) (Kent 2012). To avoid multicollinearity, only environmental variables were selected with an $R^2 < 0.75$ (Heikkinen et al. 2006). When two variables were strongly correlated (i.e. > 0.75) the variable with the higher Variance Inflation Factor (VIF) was retained (O'Brien 2007). Circular data (i.e. aspect) were transformed using trigonometric functions prior to analysis (Austin 2007).

In addition, a cluster analysis was used to identify particular species that contributed most to the dissimilarity groups between plots and between trees in the ordination space (McCune et al. 2002, McCune and Mefford 2011, Oksanen 2013). Mantel and partial Mantel tests were employed to detect how much of the species dissimilarity between plots and between trees could be attributed to environmental variables and/or geographical distance. As described by Wolf et al. (2009), spatial independence for 'epiphyte data' can be achieved by correlating geographic distance with a species distance matrix in a Mantel test, using Raup and Crick dissimilarity probability index. The Euclidean distance matrix was calculated in ArcGIS 10 and transformed using Sturge's Rule as

described by Wolf et al. (2009). A Mantel correlogram was used to visualize the spatial dependence of the sample units (Borcard and Legendre 2012).

Finally, a Species-Indicator analysis was used to identify species that were most commonly associated with different environmental and/or structural variables. The analyses were performed in the statistical program 'R' version 2.15.0 (R Developing Core Team 2011), Data Desk version 6.1 (Velleman and John 1996) and PCORD version 6.0 (McCune and Mefford 2011).

4.3. Results

A total of 7074 individuals of mechanically dependent species from 60 host trees were identified. The majority of all vascular dependent plants censured (71.5%) were infertile (having neither flowers nor fruit). 98.9% of individuals were identified to family, 95.1% to genus and 69.8% to species level. An additional 10.9% of individuals apparently matched a particular species but were not confirmed as the same (and are distinguished as 'cf.'). From the 7074 individuals, a total of 214 species from 90 different genera and 43 different families were identified (Appendix A1.1). The four families with the highest species richness and abundance were Orchidaceae, Polypodiaceae, Bromeliaceae and Araceae (Figure 4.1). The life-form group with the highest species richness and abundance was holo-epiphytes, followed by climbers, nomadic vines, primary hemi-epiphytes, mistletoes and accidental epiphytes (Table 4.1). Although stranglers were observed to have occurred in CNP (e.g. *Ficus* – Moraceae; three species by D.L. Kelly), no stranglers were found on the sampled trees.

The Chao and jackknife estimates suggested that additional species would be discovered with further sampling effort (Table 4.2). Similarly, the species accumulation curves for the different life-forms did not level off with the current sample number (Figure 4.2).

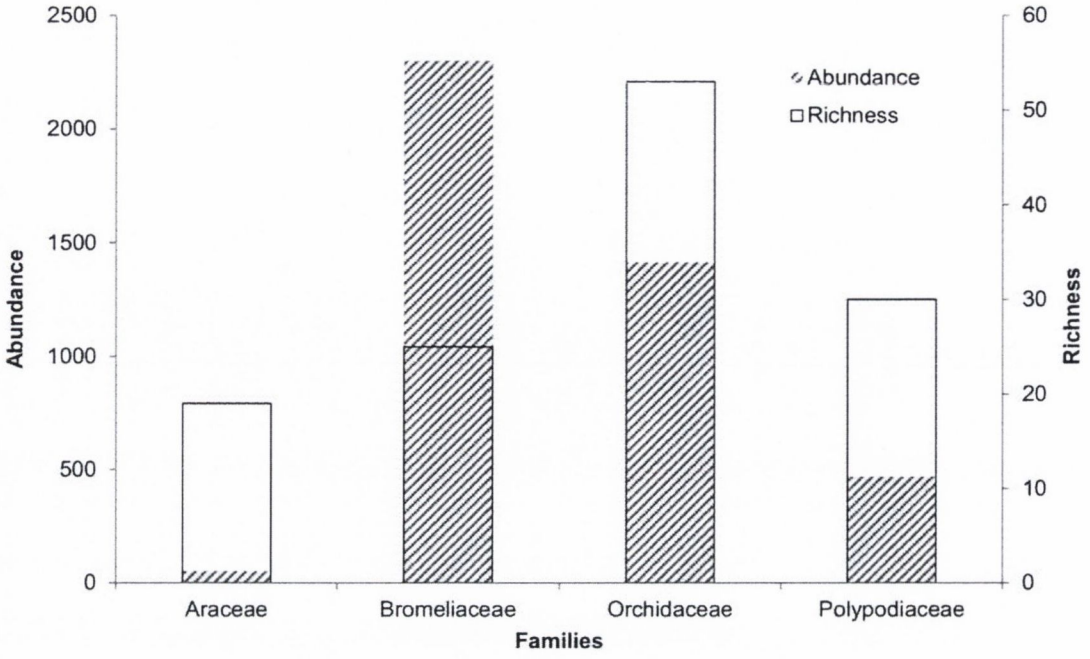


Figure 4.1 The four mechanically dependent families with the highest species abundance (no. of individuals) and richness.

Table 4.1 Overall life-form composition of the dependent flora for CNP. The total richness and abundance (no. of individuals) are given for all high (n = 5) and low (n = 5) elevation plots and the whole study area (n = 10).

Life-form	Abundance		Richness	
	Low elevation	High elevation	Low elevation	High elevation
Holo-epiphytes	2613	3910	82	85
Hemi-epiphytes	37	310	4	18
Nomadic vines	28	24	11	13
Mistletoes	36	18	2	4
Climbers	41	45	22	9
Accidental epiphytes	7	5	3	1
Stranglers	0	0	0	0
Sub-total	2762	4312	124	130
Total	7074		214	

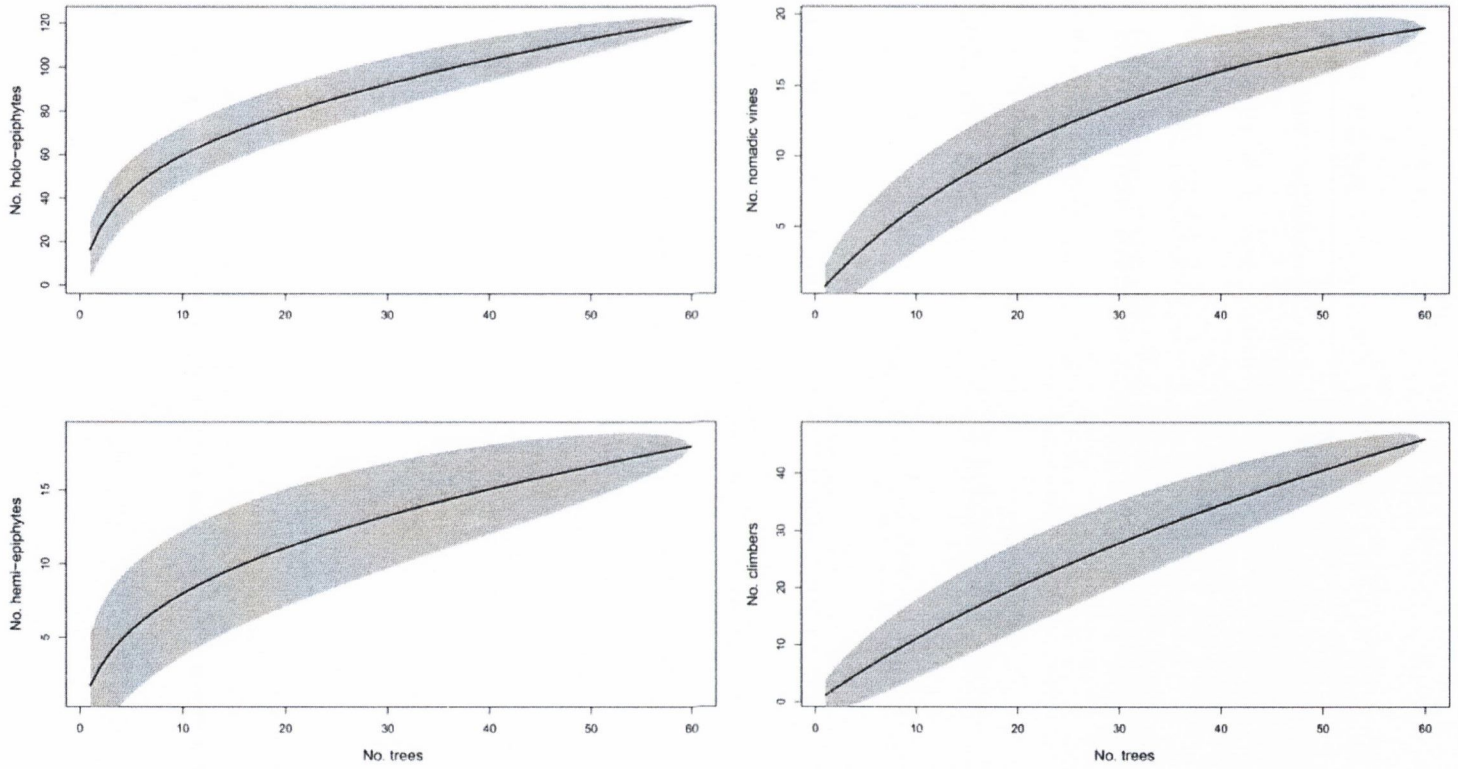


Figure 4.2 Species accumulation curves of holo-epiphytes, primary hemi-epiphytes, nomadic vines and climbers at a tree level (n = 60). The black lines represent the mean number of species and the light grey shades are the unconditional standard deviation, as used by the 'exact' method. Mistletoes and accidental epiphytes are excluded here.

Table 4.2 Species estimator results on a plot, tree and branch level using Chao and jackknife estimates.

Level	Observed number	2nd jackknife estimate	Chao estimate	Chao Variance
Plot	214	407.7	429.4	2965.3
Tree	214	399	413.4	2965.9
Branch	214	292.9	330.5	3435.7

4.3.1. Dependent floristic analysis between plots

Species richness varied greatly between different sample plots (Table 4.3). Taking all dependent taxa (including mistletoes), the highest number of species was observed at plot five (n = 76) and the lowest number at plot nine (n = 24), with a mean number of 42.8 and 60.4 species per 2.25 ha plot respectively.

Table 4.3 Mean and standard deviation of the species richness, evenness, Shannon's diversity and Simpson's diversity for the low and high elevation plots (n = 10).

		Low elevation		High elevation	
		Mean	SD	Mean	SD
Richness		42.8	19.5	60.4	13.0
Evenness		0.7	0.1	0.7	0.1
Shannon's diversity	$H' = -\sum_{i}^{S} p_i \ln(p_i)$	2.5	0.5	3.0	0.5
Simpson's diversity	$D' = 1 - \sum_{i}^{S} p_i^2$	0.8	0.1	0.9	0.1

A NMS with 500 iterations and a cluster analysis were used to identify structure in the community data between the plots. A 3-dimensional solution was recommended and a Monte Carlo test revealed an excellent representation and structure of the data (stress = 2.84) (McCune et al. 2002, Kent 2012). To test for dependent plant species dissimilarity (including mistletoes) along an environmental gradient, a second matrix was prepared that included mean VPD, elevation, aspect, slope and exposure as environmental plot variables.

Four variables were driving the species composition between plots in the ordination space, namely mean VPD, elevation, aspect and slope (Figure 4.3). A Kendall's tau rank correlation coefficient revealed that VPD had a strong negative correlation with axis 1 (r = -0.919, tau = -0.867) and with elevation (Table 4.4). Elevation had a strong positive correlation with axis 1 (r = 0.918, tau = 0.722) and aspect had a strong negative correlation with the same axis. Slope was moderate negatively correlated with axis 2 (r = -0.727, tau = -0.566; Table 4.4 and Figure 4.3; see also A4.1 and A4.4 for further summary tables). Four distinctive community groups were identified from the cluster analysis (Figure 4.4). Group one included three plots near Base Camp, group two four plots near Cantiles, group three two plots near Guanales and group four one plot between Base Camp and Cantiles (i.e. near the Operation Wallacea radio repeater). Plots that were orientated towards the SW had a higher VPD compared to plots that were orientated towards the E, W and NW. To identify whether the difference in VPD with aspect was related to past hurricane impact, we correlated VPD to plot aspect for each hurricane solution. The difference in VPD with aspect was not significantly correlated to different hurricane exposure solutions (r = 0.508, P > 0.05).

Table 4.4 Spearman's rank correlation coefficient for the NMS axis scores of the plot/species ordination. The critical value for a two-tailed r_s at α 0.05 was 0.643. Significant values are given in bold.

	Mean VPD	Elevation	Aspect	Slope	Exposure	Axis 1	Axis 2	Axis 3
Mean VPD	1							
Elevation	**-0.804**	1						
Aspect	**0.722**	-0.615	1					
Slope	0.161	-0.091	0	1				
Exposure	0.157	-0.019	0.316	0.305	1			
Axis 1	**-0.939**	**0.847**	**-0.798**	-0.253	-0.346	1		
Axis 2	0.115	-0.092	0.19	**-0.691**	0.069	0.006	1	
Axis 3	-0.358	0.043	-0.038	-0.29	-0.214	0.224	0.067	1

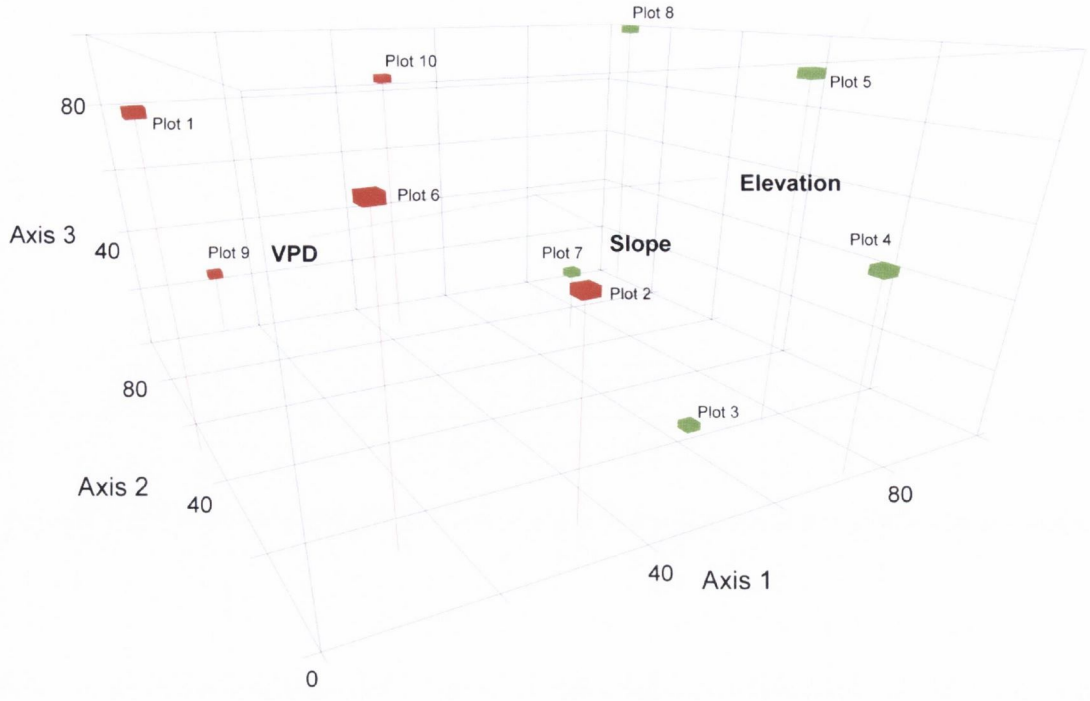


Figure 4.3 The species ordination of plots for all dependent plants (including mistletoes). The environmental variables VPD, elevation and slope were the most important variables driving the species ordination at a plot level. The red and green triangles represent the low (red) and high (green) elevation plots (note that the cluster group memberships are presented in Figure 4.4).

Using a Mantel test with Sørensen (Bray-Curtis) distance measure revealed that 44.4% ($r = 0.67$, $P < 0.01$) of the species dissimilarity between plots can be explained by the five environmental variables measured (Table A4.4). To detect the contribution of different species along different environmental conditions, a species indicator analysis was used. Each group was defined by categorical or rank-ordered quantitative environmental variables (i.e. aspect, elevation, exposure and VPD) or predefined groups (e.g. cluster groups). By combining the relative frequency and abundance of each species, an indicator value was assigned to each based on the faithfulness of their relationship to different environmental conditions. The indicator values ranged from zero (no indication) to 100 (perfect indication) and were tested for statistical significance using Monte Carlo randomizations (McCune et al. 2002). Of the five environmental variables investigated, only plot exposure showed a significant indicator group

value (Table 4.5). Of the observed exposure groups (highly exposed – highly sheltered), only one had significant indicator species associations (Table 4.6).

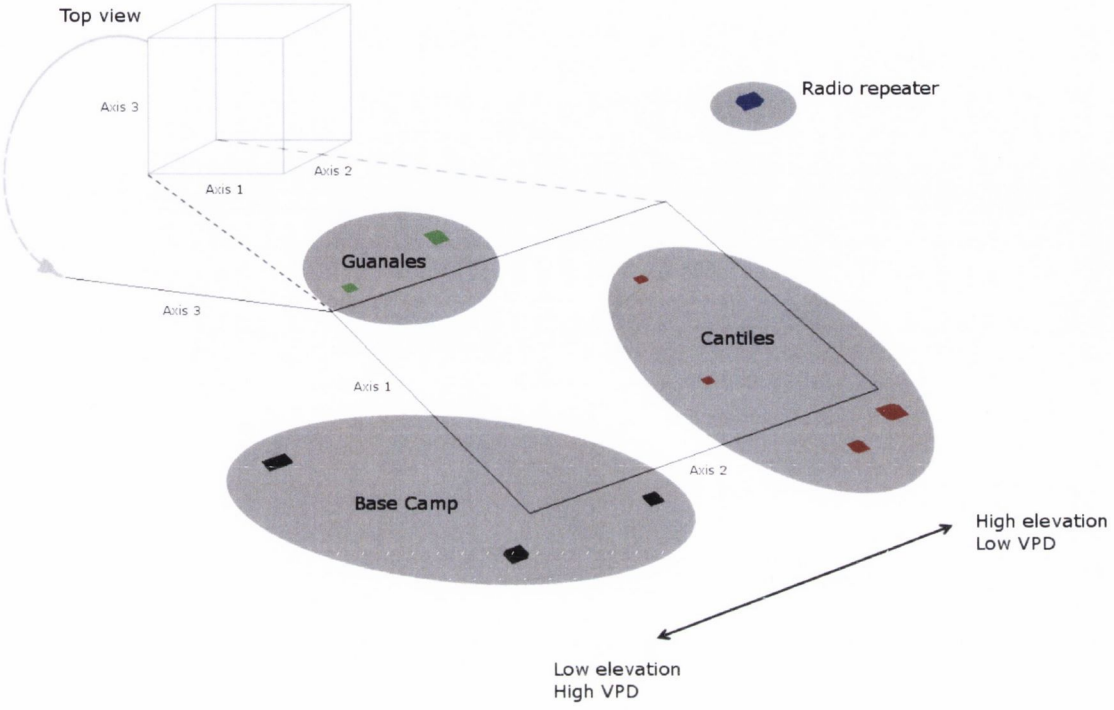


Figure 4.4 Top view of the 3-dimensional NMS scatterplot with four cluster group memberships. Each plot was treated as a sample unit (represented by colored squares). Four distinctive floristic groups were identified. Group one includes three plots (black) near Base Camp, group two four plots (red) near Cantiles, group three two plots (green) near Guanales and group four one plot (blue) between Base Camp and Cantiles. Group four was located near the Operation Wallacea radio repeater at an elevation of approximately 2000 m.

As the visual interpretation of the cluster analysis revealed two distinct vegetation clusters between low and high elevation plots, an indicator analysis was run on the two cluster groups, to identify indicator species that represented the clusters best. The species indicator analysis revealed that twelve species were distinctive indicators for the two clusters ($P < 0.01$; Table 4.7). Group one (low elevation – Figure 4.3) was strongly associated with the bromeliad *Tillandsia butzii,* the orchid *Jacquiniella teretifolia* and the fern *Serpocaulon*

triseriale, whereas group two (high elevation – Figure 4.3) was associated with the remaining nine species (Table 4.7).

Table 4.5 Monte Carlo test results of significance for the observed and mean indicator value (IV) of the environmental variables at plot level.

Variables	Mean obs. indicator value (IV)	Obs. sum	P-value
Aspect	31.66	6902.1	>0.05
Elevation	42.58	9281.4	>0.05
Exposure	40.43	8812.7	<0.05*
VPD	36.21	7891.1	>0.05
Slope	37.71	8220.4	>0.05

Table 4.6 Indicator values of the different plot exposure levels. Monte Carlo results are presented. Group 1 comprised four sheltered plots; whereas group 2 comprised two moderately exposed plots.

	Sheltered [n=4]	M. sheltered [n=2]	M. exposed [n=2]	Exposed [n=2]				
Species	**Group 1 (%)**	**Group 2 (%)**	**Group 3 (%)**	**Group 4 (%)**	**IV**	**Mean**	**StD**	**P-value**
Catopsis montana	0	100	0	0	99.9	48.8	21.99	0.048
Clusia minor	0	99	0	0	98.9	46.9	21.6	0.044
Dichaea neglecta	2	92	0	0	92.3	43.8	21.42	0.048
Elaphoglossum muscosum	6	89	0	0	88.9	47.9	21.06	0.045
Tillandsia guatemalensis	9	88	0	0	87.8	52.1	19.24	0.044

4.3.2 Dependent floristic analysis between trees

The majority of the 60 mature trees that were surveyed belonged to *Liquidambar styraciflua* (n = 22), *Pinus* spp. (n = 18) and *Quercus* spp. (n = 9) (Table 4.8). Structural properties varied between trees (Table 4.9 and 4.10). Mean tree height was 40.4 m with a mean surface area of 163.9 m^2. The total surface area surveyed (i.e. branches that hosted vascular dependent plants) was 9836.5 m^2, with a mean number of 20.7 dependent plant species per trees. *Pinus* spp. had the highest total surface area, followed by *Liquidambar, Quercus, Cedrela* and other trees (Table 4.10). Individuals of *Pinus* had the greatest mean bole height, with a relatively symmetrical and excurrent canopy

(Figure 4.5). Most branches of *Pinus* were located in the upper part of the canopy (Figure 4.6). Individuals of *Liquidambar* had an excurrent canopy (Figure 4.6). The canopy was mostly orientated towards the west, with most branches being located in the mid and upper canopy (Figure 4.5). Individuals of *Cedrela* had a similar canopy arrangement to *Liquidambar.* However, *Cedrela* trees had a larger decurrent canopy. *Quercus* spp. were the shortest trees surveyed, with the lowest branch canopy, lowest mean bole height and a decurrent canopy (Figure 4.6).

Table 4.7 Indicator values of the two cluster groups for high and low elevation plots (n = 10). Monte Carlo results and indicator values including percentage contribution of each species are presented. The values above the group number represent the cluster group membership (1 = low elevation; 3 = high elevation) and the total number of plots included in the analysis. Group one comprised plots 1, 2, 6, 9 and 10. Group two comprised plots 3, 4, 5, 7 and 8. IV = Indicator Value (100 = perfect indication).

	Low elevation (1) [n=5]	High elevation (3) [n=5]		[n=10]		
Species	**Group 1 (%)**	**Group 2 (%)**	**IV**	**Mean**	**StD**	**P-value**
Jacquiniella teretifolia	93	7	92.9	68.1	10.89	0.04
Tillandsia butzii	92	8	92.3	67.1	11.4	0.02
Serpocaulon triseriale	80	0	80	37	14.56	0.05
Tillandsia vicentina	6	94	94.2	69.2	15.99	0.03
Werauhia werckleana	5	92	92.4	54.8	11.76	0.01
Tillandsia lampropoda	3	95	95.1	58	14.18	0.01
Macleania insignis	3	83	82.5	44.5	13.71	0.04
Tillandsia guatemalensis	2	95	95.3	52.5	14.04	0.01
Serpocaulon lasiopus	0	100	100	42.1	14.07	0.01
Clusia minor	0	80	80	38.6	15.08	0.05
Sphyrospermum cordifolium	0	80	80	37.2	16.17	0.05
Tillandsia standleyi	0	80	80	41.1	16.22	0.05

A Mantel test was used to test how the dependent plant community composition (including mistletoes) changed with distance between trees (Table A4.4). The test revealed that the species matrix was strongly correlated with the geographical distance matrix ($r = 0.205$, $P < 0.05$ with 999 permutations). A correlogram with five distance classes indicated that dependent plant populations distant by < 500 m tend to be similar, with a more or less linear

decrease (although not constantly significant; Figure 4.7) to a value of -0.17 ($P < 0.05$) in the last distance class (approximately 6170 m).

Table 4.8 Number of mature tree species surveyed (n = 60) within each family. Note that *Liquidambar* was formerly classed into Hamamelidaceae.

Family	Species	Total number
Altingiaceae	*Liquidambar styraciflua* L.	22
Aquifoliaceae	*Ilex pallida* Standl.	1
Araliaceae	*Dendropanax* sp.	1
Fagaceae	*Quercus* cf. *benthamii* A. DC.	1
Fagaceae	*Quercus* cf. *lancifolia* Liebm. ex A. DC.	3
Fagaceae	*Quercus* cf. *xalapensis* Bonpl.	1
Fagaceae	*Quercus cortesii* Liebm.	4
Juglandaceae	*Oreomunnea* sp.	1
Lauraceae	*Persea* sp.	1
Meliaceae	*Cedrela odorata* L.	5
Pinaceae	*Pinus maximinoi* H.E. Moore	14
Pinaceae	*Pinus tecunumanii* F. Schwerdtf. ex Eguiluz & J.P.Perry	4
Rosaceae	*Prunus rhamnoides* Koehne	1
Sabiaceae	*Meliosma corymbosa* A.H. Gentry	1

Table 4.9 Structural summary of the 60 sampled trees.

	Circumference (m)	Height (m)	Canopy diameter (m)	Surface area (m^2)
Mean	3.1	40.4	15.0	163.9
Min.	1.6	20.5	8.9	46.8
Max.	5.3	62.0	26.2	410.1
StD.	0.8	9.9	3.5	83.0
Total	186.1	2425.2	897.1	9836.5

Table 4.10 Mean and total branch surface area for the principal tree species (n = 60).

Species	Mean surface area (m^2)	Total (m^2)
Cedrela odorata [n=5]	171.3	856.5
Liquidambar styraciflua [n=22]	150.3	3306.2
Others [n=6]	518.1	518.1
Pinus spp. [n=18]	465.7	4128.9
Quercus spp. [n=9]	449.0	1026.9
Total		9836.5

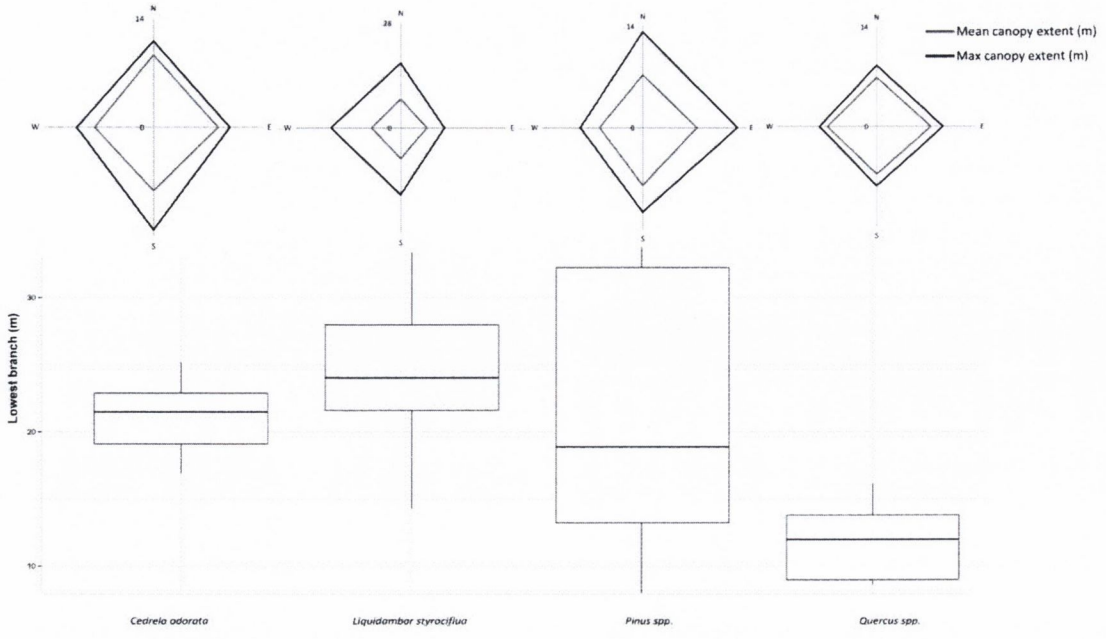


Figure 4.5 Mean, maximum and minimum length of the lowest recorded branches of the four principal tree species. Note that the lowest branch does not always indicate the height of the bole (see Figure 4.6 for comparison). The radar-diagrams above the bars represent the mean and maximum canopy extent for the four cardinal directions.

A partial Mantel test was used to assess whether site environmental variables would reduce the spatial dependence between the trees (i.e. the site environmental variables could potentially reduce the importance of geographical distance). The environmental distance matrix was used as a covariable and combined with the species and the geographical distance matrix. The environmental variables entered were tree type (i.e. angiosperms and conifer), elevation, tree circumference, tree height, canopy extent (N, W, E and S), canopy openness, branch surface area and the predicted EVSS for four cardinal model solutions (S, SE, NE and NW). Note that only the EVSS South and South-East solutions are presented here, as these solutions were the best fit model solutions. The partial Mantel test was based on Pearson's product-moment correlation and revealed that 48.4% of the dependent plant similarity between trees could be explained by the environmental and geographical distance data ($P < 0.01$). Geographic distances between trees explained most of the similarity ($r = 0.645$, 41.6%), followed by environmental variables ($r =$

0.261, 6.8%). 15.6% of the variation was shared by environmental variables and geographical distance (Table A4.4).

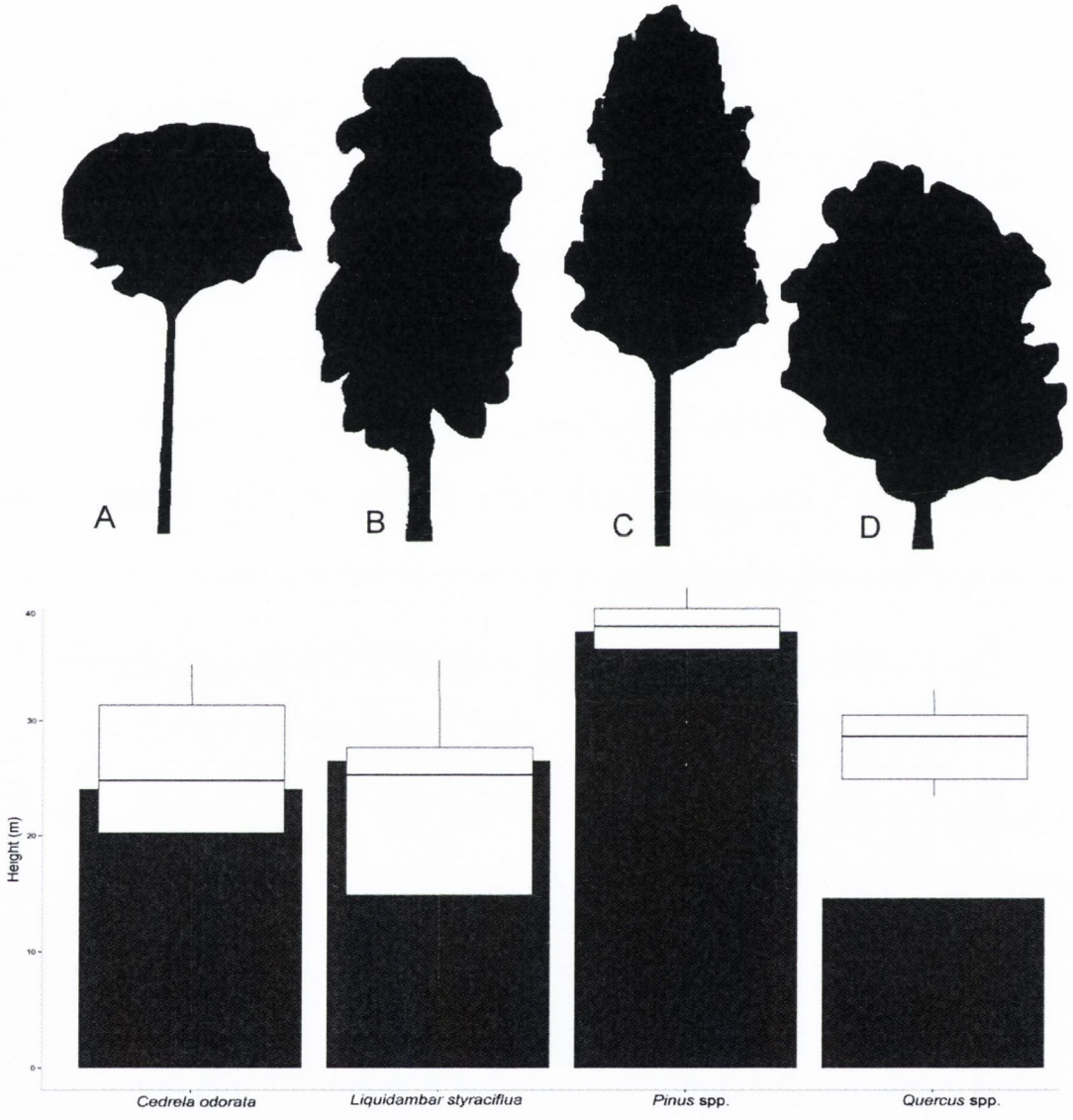


Figure 4.6 Boxplot of mean canopy depth and bar plot (black) of mean bole height for the four principal tree species. The above tree images represent the general canopy shape of the four principal tree species [A = *Cedrela* (decurrent corwn); B = *Liquidambar* (excurrent crown); C = *Pinus* (excurrent crown); D = *Quercus* (decurrent crown)].

To test how mechanically dependent plant species richness and diversity changed along a gradient of hurricane impact between individual trees, between different tree types and with canopy openness, a Spearman's rank correlation coefficient with an ANOVA pairwise-comparison was used. Dependent plant diversity, using Simpson's diversity index (rho = -0.68, $P < 0.01$), Shannon's diversity index (rho = -0.65, $P < 0.01$) and species richness (rho = -0.57, $P < 0.01$) decreased with increasing predicted hurricane damage (Figure 4.8 shows the results for the Simpson's index only). Note, that the two different diversity indices were used for comparison purposes only. Species richness and diversity were negatively correlated with increased canopy openness (richness: rho = -0.369, $P < 0.01$; Simpson's diversity: rho = -0.531, $P < 0.01$). Pairwise comparisons revealed that closed canopies were significantly different (both in terms of diversity and species richness) compared to intermediate and open canopies. However, intermediate canopies did not significantly differ from open canopies. Furthermore, dependent plant Simpson's diversity (but not richness) was compared with tree type: conifer trees had a significantly lower dependent plant diversity compared to angiosperm trees (Simpson's diversity: rho = -0.311, $P < 0.05$, conifer D' = 0.79 versus angiosperms D' = 0.84; richness: rho = -0.221, $P > 0.05$).

Dependent plant richness and abundance declined significantly with branch circumference (log richness: $P < 0.01$, $R^2 = 0.62$; log abundance: $P < 0.01$ $R^2 = 0.78$). Dependent plant abundance and richness did not change with branch circumference when compared among trees at different hurricane exposure sites ($P > 0.05$).

To test the effect of different hurricane exposure solutions on the abundance and richness of different life-forms we compared different exposure sites. The solution with the lowest AIC (i.e. best fit solution) was the south model. A Tukey Honest significant test was used to compare confidence intervals on the differences in abundance and richness among factors (hurricane solution and life-forms). Richness of holo-epiphytes ($t = -6.78$, $P < 0.01$) and primary hemi-epiphytes ($t = -2.89$, $P < 0.01$) were negatively related with increasing hurricane impact. All other comparisons of richness with life-forms were non-significant

(climbers: t = 0.13, P > 0.05; nomadic vines: t = -1.1, P > 0.05; mistletoes: t = -0.25, P > 0.05). Abundance of different life-forms did not change with hurricane impact (holo-epiphytes: t = -1.2, P > 0.05; climbers: t = 0.03, P > 0.05; nomadic vines: t = -0.11, P > 0.05; mistletoes: t = -0.05, P > 0.05; primary hemi-epiphytes: t = -0.86, P > 0.05).

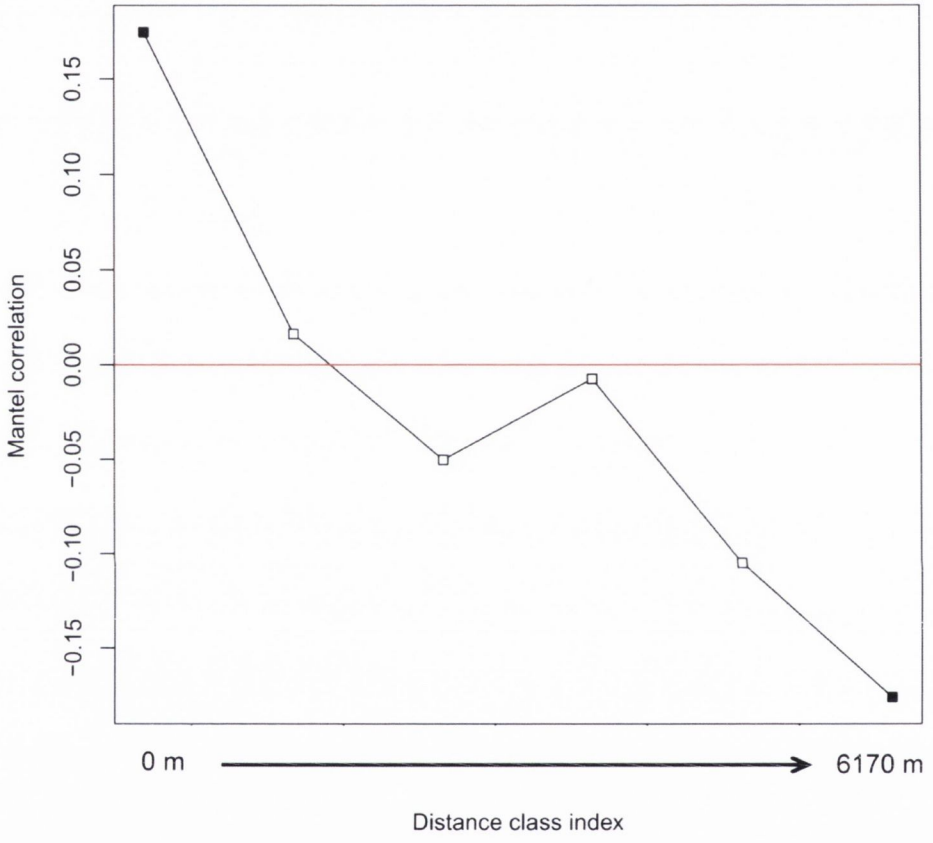


Figure 4.7 Mantel correlogram of the dependent plant species matrix for 60 trees (r = 0.205, P < 0.05). A species and geographical distance matrix was used based on Raup and Crick probabilistic coefficient. The distance class index represents the distance range between zero and 6170 m. Solid symbols indicate a significant value of Mantel r (P < 0.05).

4.3.3 Cluster separation

As elevation had a strong overall effect on the vegetation clustering in the ordination space, elevation was excluded as an environmental variable and the

species data were analyzed separately for the two clusters (Figure 4.3). This was done to identify other environmental variables that might affect the vegetation composition (including mistletoes) between trees in the absence of large elevation ranges. Cluster one (low elevation) consisted of 121 dependent species on 30 trees, whereas cluster two (high elevation) consisted of 129 dependent species on 30 trees (excluding accidental epiphytes).

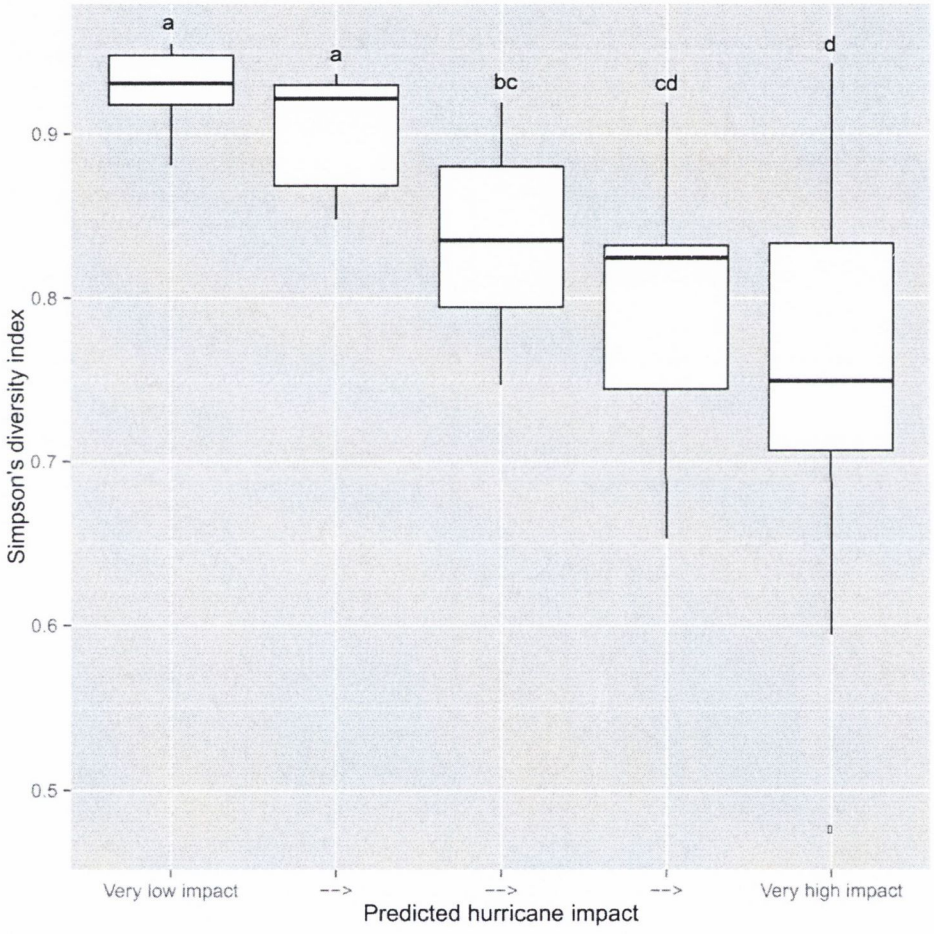


Figure 4.8 Boxplot of the Simpson's diversity index in relation to predicted hurricane impact for the EVSS south solution (best fit solution). Significant differences ($\alpha = 0.05$) between impact levels are indicated by letters.

4.3.3.1. Cluster one – low elevation trees

For cluster one a 2-dimensional solution was recommended (stress value = 11.49). Following visual assessment of the cluster analysis, cluster one was subdivided into four sub-clusters. To test the influence of other environmental variables on the dependent plant composition between trees in the 'absence' of strong elevation effects, a Mantel test with Sørensen (Bray-Curtis) distance measure was used. The test revealed that 30% ($r = 0.547$, $P < 0.01$) of the species dissimilarity between trees can be explained by the 13 environmental variables (Table A4.4). Axis 1 was strongly negatively correlated with the south and southeast hurricane EVSS (Table 4.11, Table A4.2). The south and southeast hurricane solutions represent the hurricane exposure scores that were validated as explaining most of the observed tree damage on the ground (Chapter 2). The correlation with axis 1 suggests that the dependent plant community composition was affected along the gradient of hurricane exposure. Canopy openness was moderately negatively correlated with axis 2 and moderately positively correlated with tree type (i.e. angiosperm trees had a more closed canopy than conifers), canopy extent north and tree circumference. Tree type was negatively correlated with both axes and positively correlated with the EVSS southeast solution (Table 4.11, Table A4.2).

Table 4.11 Spearman's rank correlation coefficient for the NMS axis scores of the tree/species ordination of the low elevation cluster (group one). The critical value for a two-tailed r_s at α 0.05 was 0.336. Significant values are given in bold. Variables that were not significantly correlated with other variables were excluded here (e.g. canopy extent south and west). Circ. = tree circumference; C. ext. = canopy extent; EVSS = 'exposure vulnerability site score' derived from the hurricane model.

	Tree type	Circ.	Height	C. ext. (N)	C. ext. (E)	Openness	Surf. area	EVSS (S)	EVSS (SE)	Axis 1	Axis 2
Tree type	1										
Circ.	1.46	1									
Height	0.071	**0.496**	1								
C. ext. (N)	0.217	**0.577**	**0.336**	1							
C. ext. (E)	**0.353**	0.196	0.266	**0.461**	1						
Openness	**0.494**	**0.765**	0.51	**0.586**	0.217	1					
Surf. area	0.281	-0.14	-0.178	0.067	0.05	-0.027	1				
EVSS (S)	0.129	-0.35	**-0.341**	-0.179	-0.33	-0.299	**0.429**	1			
EVSS (SE)	**0.475**	-0.319	**-0.388**	0.023	-0.031	-0.126	0.5	**0.754**	1		
Axis 1	**-0.525**	0.227	0.324	-0.091	-0.09	0.092	**-0.404**	**-0.455**	**-0.825**	1	
Axis 2	**-0.353**	**-0.534**	**-0.456**	**-0.552**	-0.233	**-0.732**	0.071	0.238	-0.046	0.034	1

To investigate which dependent plant species contribute to the vegetation clustering in the ordination space for cluster one, a species indicator analysis was applied with Monte Carlo randomization. As was previously done, each environmental variable and cluster group was tested for significant indicator values. Following visual assessment, a sub-cluster group with four clusters was selected to be the best representation. Several indicator species were associated with each of these four sub-clusters (Table 4.12). Group one was moderately associated with the orchid *Epidendrum mixtum* and the bromeliads *Tillandsia seleriana* and *Tillandsia butzii*. Group two was weakly associated with indicator species *Werauhia werckleana* (bromeliad) and *Pleopeltis crassinervata* (fern). Group three was strongly associated with the ferns *Elaphoglossum guatemalense*, *Elaphoglossum clewellianum* and *Melpomene anfractuosa*. Finally, group four was strongly associated with the orchid *Dinema polybulbon* (Table 4.12). Group one and two consisted of trees from plots that were sampled near Base Camp, whereas group three and four consisted of trees from plots that were sampled near the Guanales camp site.

Of the 13 environmental variables investigated, five had significant indicator species associations (Table 4.13). The two most important environmental variables were tree type and hurricane impact (e.g. EVSS south-east). Four of the five EVSS classes (i.e. 1, 2, 3, 4 and 5) had significant indicator species associations (Table 4.14). Group one (EVSS 5 = very high impact) consisted of one significant species association, namely the bromeliad *Tillandsia seleriana*. Group two (EVSS 4 = high impact) had one moderate-weakly associated indicator species (the fern *Polypodium plesiosorum*). Groups three and four (EVSS 1 and 2 = very low and low impact) had ten moderate to very faithful indicator species (Table 4.14).

The division into the two different tree types (i.e. angiosperms and conifer) yielded different species indicator associations. Angiosperm trees were moderately associated with the orchid *Jacquiniella teretifolia* and weakly associated with *Struthanthus orbicularis* (a mistletoe). Conifer trees on the other hand were moderately associated with the Bignoniaceous climber *Thunbergia*

aff. *alata,* the bromeliads *Catopsis hahnii* and *Tillandsia seleriana* and the orchid *Epidendrum mixtum* (Table 4.15).

Table 4.12 Indicator values of species for the four sub-clusters from cluster one (low elevation). Monte Carlo results and indicator values including percentage contribution of each species are presented. The values above the group numbers represent the cluster group membership and the total number of trees included in the analysis. IV = Indicator Value (100 = perfect indication).

	[n=9]	[n=6]	[n=7]	[n=5]				
Species	**Group 1 (%)**	**Group 2 (%)**	**Group 3 (%)**	**Group 4 (%)**	**IV**	**Mean**	**StD**	**P-value**
Epidendrum mixtum	78	0	0	0	77.8	21.6	9.99	0.001
Tillandsia butzii	63	26	9	1	62.6	34.6	5.59	0.000
Tillandsia seleriana	62	16	0	0	61.9	31.6	11.73	0.018
Rhynchostele cordata	56	0	0	0	55.6	19.3	9.97	0.006
Epidendrum ramosum	48	1	29	15	48.5	34.4	6.73	0.037
Jacquiniella teretifolia	22	0	51	24	50.9	34.6	8.5	0.048
Prosthechea rhynchophora	20	0	54	2	54.4	30.2	9.5	0.021
Tillandsia magnusiana	5	39	0	0	39.5	18.3	9.08	0.036
Werauhia werckleana	4	55	0	0	54.5	19.3	8.95	0.006
Pleopeltis crassinervata	0	50	0	0	50	16.8	9.23	0.010
Smilax domingensis	2	43	0	0	42.9	17.2	9.33	0.029
Elaphoglossum guatemalense	1	0	92	0	91.9	28.1	10.89	0.000
Maxillaria neglecta	1	0	67	0	67.4	20.7	9.96	0.002
Stelis immersa	1	0	54	0	54.3	19.3	9.99	0.010
Elaphoglossum clewellianum	0	0	86	0	85.7	19.8	9.32	0.000
Melpomene anfractuosa	0	0	84	0	84	21.9	10	0.000
Macleania insignis	0	0	71	0	71.4	19.2	9.78	0.001
Stelis guatemalensis	0	0	64	2	64	20.3	9.71	0.003
Pleopeltis mexicana	0	0	57	0	57.1	19.9	10.24	0.010
Dichaea glauca	0	0	43	0	42.9	16.1	9.24	0.023
Pleopeltis angusta	0	0	43	0	42.9	15.3	9.24	0.023
Polypodium plesiosorum	0	0	43	0	42.9	16	9.34	0.024
Stelis sp. 1	0	0	43	0	42.9	15.7	8.97	0.019
Vittaria sp. 1	0	0	43	0	42.9	17.2	9.17	0.021
Struthanthus orbicularis	0	0	30	58	58.3	23.3	8.29	0.003
Dinema polybulbon	0	0	0	97	96.6	21.6	10.45	0.000

4.3.3.2. Cluster two – high elevation trees

Cluster two was analyzed in the same way as cluster one. The NMS with Monte Carlo configuration suggested a 2-dimensional solution (stress value = 14.92). The trees in cluster two were grouped into four sub-clusters following the inspection of the cluster analysis results.

Table 4.13 Monte Carlo tests of significance of mean indicator value (IV) for the sub-cluster groups and environmental variables of cluster group one (low elevation) and two (high elevation). Randomizations could not be performed on some variables due to the lack of data (signified as 'na').

	Low elevation		High elevation	
Variables	IV	P-value	IV	P-value
Tree type	9.3	<0.01*	11.11	>0.05
Circumference	11.69	<0.05*	12.38	>0.05
Height	15.97	<0.05*	21.84	>0.05
Canopy extent (W)	na	na	16.15	>0.05
Canopy extent (S)	na	na	15.91	>0.05
Canopy extent (N)	14.24	>0.05	17.48	>0.05
Canopy extent (E)	11.92	>0.05	14.45	>0.05
Canopy Openness	9.48	>0.05	12.65	<0.01*
Area	na	na	13.87	>0.05
EVSS S	13.01	<0.01*	15.96	<0.01*
EVSS SE	16.19	<0.01*	14.69	<0.05*
4 cluster groups	14.55	<0.01*	17.32	<0.01*

Table 4.14 Indicator values of species in relation to level of predicted hurricane damage at low elevation sites. Monte Carlo results and indicator values including percentage contribution of each species are presented. The values above the group represent the predicted hurricane damage scores (1 = very low impact; 5 = very high impact) and the total number of trees included in the analysis. IV = Indicator Value (100 = perfect indicator).

Predicted hurricane damage	Very low impact → Very high impact							
EVSS class:	1 [n=5]	2 [n=2]	4 [n=6]	5 [n=13]				
Species	**Group 3 (%)**	**Group 4 (%)**	**Group 2 (%)**	**Group 1 (%)**	**IV**	**Mean**	**StD**	**P-value**
Dinema polybulbon	74	0	1	0	74.4	24.5	13.98	0.02
Melpomene onfractuosa	3	69	12	0	69.2	26.7	13.56	0.03
Macleania insignis	2	83	2	0	82.8	24	13.32	0.01
Elaphoglossum guatemalense	2	82	9	0	82.3	32.7	14.48	0.01
Elaphoglossum clewellianum	2	71	10	0	70.9	24.7	13.01	0.02
Arpophyllum giganteum	1	71	4	0	71.1	22.5	13.51	0.02
Pleurothallis matudana	0	100	0	0	100	19.4	11.92	0.00
Syngonium podophyllum	0	100	0	0	100	19.4	11.92	0.00
Stelis sp. 1	0	94	1	0	93.8	20.9	12.87	0.00
Stelis immersa	0	91	3	0	91.2	24	13.69	0.00
Maxillaria neglecta	0	64	17	0	63.9	25.1	13.43	0.03
Polypodium plesiosorum	0	0	50	0	50	21	12.68	0.02
Tillandsia seleriana	0	3	0	77	77.4	35.9	14.36	0.02

Table 4.15 Indicator values of species for two different tree types (n = number of trees included in the analysis) within cluster one (low elevation). Monte Carlo results and indicator values including percentage contribution of each species are presented.

	Angiosperms [n=18]	Conifer [n=9]				
Species	**Group 1 (%)**	**Group 2 (%)**	**IV**	**Mean**	**StD**	**P-value**
Jacquiniella teretifolia	72	5	72.5	48.6	9.14	0.016
Struthanthus orbicularis	56	0	55.6	28.3	8.2	0.010
Thunbergia aff. *alata*	19	79	78.8	55	6.78	0.003
Tillandsia seleriana	3	71	71.1	37	10.06	0.003
Catopsis hahnii	0	78	77.8	22.5	8.22	0.000
Epidendrum mixtum	0	78	77.8	22.6	8.08	0.000
Rhynchostele cordata	0	42	42.3	17.9	7.37	0.011
Satyria warszewiczii	0	33	33.3	13.4	5.93	0.031

The same environmental variables were tested as in cluster one (see above). A Mantel test with Sørensen (Bray-Curtis) distance measure revealed for cluster group two that 30% ($r = 0.547$; $P < 0.01$) of the species dissimilarity between trees was explained by the environmental variables in the 'absence' of strong elevation effects (Table A4.4). In the NMS, axis 1 was weakly positively correlated with canopy openness and weakly negatively correlated with tree height (Table 4.16). Axis 2 was weakly to moderately positively correlated with hurricane exposure (EVSS south and southeast), canopy openness, tree surface area, tree height, circumference and tree type. Additionally, tree surface area was strongly positively correlated with tree circumference and height and weakly positively correlated with tree type. Canopy openness was moderately positively correlated with tree type and hurricane exposure (EVSS south and southeast). Conifer trees had a more open canopy compared to angiosperm trees. Canopy openness increased with hurricane EVSS. Finally, canopy extent (south and east) was weakly positively correlated with tree surface area (Table 4.16, Table A4.2).

Table 4.16 Spearman's rank correlation coefficient for the NMS axis scores of the tree/species ordination of the high elevation cluster (cluster two). The critical value for a two-tailed r_s at α 0.05 was 0.301. Significant values are given in bold. Circ. = tree circumference; C. ext. = canopy extent; EVSS = 'exposure vulnerability site score' derived from the hurricane model; C. openness = canopy openness.

	Tree type	Circ.	Height	C. ext. (N)	C. ext. (W)	C. ext. (S)	C. ext. (E)	C. openness	Surface area	EVSS (S)	EVSS (SE)	Axis 1	Axis 2
Tree type	1												
Circ.	**0.411**	1											
Height	**0.329**	**0.794**	1										
C. ext. (N)	-0.143	0.276	0.235	1									
C. ext. (W)	**-0.368**	0.077	0.059	0.249	1								
C. ext. (S)	0.075	0.39	**0.44**	0.049	0.247	1							
C. ext. (E)	-0.114	0.251	0.232	0.187	0.156	**0.386**	1						
C. openness	**0.601**	0.215	0.044	-0.291	-0.082	-0.06	-0.235	1					
Surface area	**0.443**	**0.889**	**0.877**	0.262	0.123	**0.47**	**0.378**	0.153	1				
EVSS (S)	**0.589**	0.175	0.255	**-0.466**	-0.273	-0.092	-0.199	**0.726**	0.287	1			
EVSS (SE)	**0.436**	0.101	0.214	**-0.364**	**-0.33**	-0.059	-0.193	**0.557**	0.21	**0.891**	1		
Axis 1	0.171	-0.208	**-0.462**	-0.123	0.139	-0.123	0.111	**0.417**	-0.268	0.05	-0.022	1	
Axis 2	**0.514**	**0.539**	**0.599**	-0.066	0.039	0.182	0.064	**0.609**	**0.607**	**0.65**	**0.588**	0.024	1

In the case of cluster two, only three environmental variables (i.e. EVSS south and southeast and canopy openness) had strong significant indicator species associations (Table 4.13). The sub-cluster with four groups had significant species associations (Table 4.17). A total of ten species were associated with group one. However, only two species were strong indicators for these groups, namely the ferns *Elaphoglossum petiolatum* and *Melpomene xiphopteroides*. Group two had three moderately significant indicator species and group three had one (*Maxillaria cucullata*, *Sphyrospermum cordifolium* and *Elaphoglossum muscosum*). Group four was strongly associated with the bromeliads *Catopsis montana* and *Tillandsia standleyi* (Table 4.17). Groups one, two and three were associated with trees in plots sampled near the Cantiles camp site. Group four was associated with trees sampled in one plot between Base Camp and the camp site Cantiles (the radio repeater; Figure 4.4).

Canopy openness and hurricane EVSS for the south solution were the two environmental variables with the highest significant indicator values. The grouping of the EVSS south solution identified indicator species for all five impact levels (Table 4.18). High impact sites (EVSS = 5) had generally fewer indicator species compared to very low impact sites (EVSS = 1). Moreover, highly affected sites had weaker indicator associations compared to low impact sites. The species with the highest indicator value for the low impact sites was the fern *Pleopeltis mexicana* (strongly associated), whereas the species with the highest indicator value for the exposed sites was the orchid *Epidendrum ramosum* (moderate association) (Table 4.18).

Finally, the environmental variable 'canopy openness' was associated with particular indicator species (Table 4.19). Closed canopies had significantly higher numbers of indicator species compared to trees with open canopies. Many ferns were associated with closed canopy cover, whereas species such as the orchids *Stelis villosa* and *Encyclia tuerckheimii* were more associated with open canopies (Table 4.19).

Table 4.17 Indicator values of species for the four sub-clusters from the high elevation plots (cluster two). Monte Carlo results and indicator values including percentage contribution of each species are presented. The values above the group number represent the cluster group membership and the total number of trees included in the analysis. IV = Indicator Value (100 = perfect indication).

	[n=12]	[n=12]	[n=3]	[n=6]				
Species	**Group 1 (%)**	**Group 2 (%)**	**Group 3 (%)**	**Group 4 (%)**	**IV**	**Mean**	**StD**	**P-value**
Melpomene xiphopteroides	79	7	0	0	78.9	30.2	10.57	0.001
Elaphoglossum petiolatum	79	1	0	0	78.7	24.9	10.3	0.000
Tillandsia multicaulis	52	15	6	0	52.4	30.2	9.13	0.034
Stelis immersa	50	0	0	0	50	19.3	10.35	0.022
Pleurothallis matudana	45	3	4	0	45	23.7	10.39	0.042
Tillandsia punctulata	30	66	2	0	66.4	31.9	5.98	0.000
Epidendrum ramosum	26	62	1	5	62.3	33.9	6.74	0.001
Sphyrospermum cordifolium	23	2	45	0	45.3	24.1	10.58	0.039
Tillandsia vicentina	9	77	7	1	77.4	34.4	7.44	0.000
Vittaria sp. 1	2	1	0	68	67.7	22.5	10.92	0.007
Melpomene anfractuosa	0	5	14	60	60.1	27.2	10.69	0.015
Catopsis montana	0	5	7	82	81.9	26.8	10.26	0.000
Elaphoglossum muscosum	0	4	23	62	61.5	24.1	9.88	0.007
Tillandsia standleyi	0	4	10	79	79.1	26.5	10.06	0.000
Maxillaria cucullata	0	0	63	0	62.7	16	9.07	0.004
Encyclia tuerckheimii	0	0	4	29	29.4	15.8	9.31	0.043
Nephrolepis cordifolia	0	0	0	48	47.8	17.7	10.33	0.026
Lepanthes vilchezii	0	0	0	33	33.3	14	8.87	0.033
Prestonia cf. *portobellensis*	0	0	0	33	33.3	14	8.83	0.036
Prosthechea vitellina	0	0	0	33	33.3	14.1	8.46	0.036

Table 4.18 (next page) Indicator values of species in relation to level of predicted hurricane damage at high elevation sites. Monte Carlo results and indicator values including percentage contribution of each species are presented. The values above the group number represent the total number of trees included in the analysis and the EVSS level. IV = Indicator Value (100 = perfect indication).

Predicted hurricane damage	Very low impact →				Very high impact				
EVSS class:	1 [n=6]	2 [n=9]	3 [n=6]	4 [n=8]	5 [n=4]				
Species	**Group 4 (%)**	**Group 5 (%)**	**Group 1 (%)**	**Group 3 (%)**	**Group 2 (%)**	**IV**	**Mean**	**StD**	**P-value**
Pleopeltis mexicana	82	2	2	0	0	82	23.2	9.94	0.000
Peperomia sp. 1	59	1	0	0	0	58.8	16.1	8.68	0.002
Elaphoglossum petiolatum	53	3	9	0	1	53.1	22.6	9.18	0.012
Tillandsia multicaulis	51	13	2	1	15	50.9	26.5	7.58	0.008
Monstera adansonii	50	0	0	0	0	50	14.4	8.36	0.007
Selaginella schizobasis	50	0	0	0	0	50	14.8	8.77	0.011
Pleurothallis matudana	43	1	4	0	7	43.4	21.6	8.87	0.026
Asplenium radicans	42	1	0	1	0	42.5	18.8	9.92	0.020
Elaphoglossum clewellianum	40	15	1	6	3	40	22.9	7.04	0.031
Stelis immersa	40	1	5	0	0	39.7	17.6	9.3	0.030
Macleania insignis	22	20	4	37	5	36.5	27	4.74	0.039
Werauhia werckleana	21	35	6	32	2	34.6	27.1	4.1	0.048
Rhynchostele cordata	15	2	7	2	55	55.1	25.4	7.7	0.003
Tillandsia guatemalensis	12	22	4	38	2	38.4	26.9	5.99	0.048
Phlebodium pseudoaureum	9	4	57	12	0	56.6	25.6	7.38	0.001
Epidendrum ramosum	8	6	17	11	52	51.7	29.1	5.65	0.001
Tillandsia butzii	2	4	58	3	13	58.2	27.5	8.44	0.004
Anthurium scandens	2	1	36	1	0	35.6	17.6	8.91	0.036
Clusia minor	0	42	6	6	0	41.5	21.8	8.42	0.030
Elaphoglossum muscosum	0	19	2	42	0	42.4	21	7.82	0.020
Tillandsia standleyi	0	13	3	49	0	48.6	23.1	8.12	0.011
Catopsis montana	0	7	11	49	0	49.4	23.4	8.41	0.014
Clusia cf. *flava*	0	1	0	0	46	45.9	14.9	8.74	0.010

Table 4.19 Indicator values of species in relation to level canopy openness at high elevation sites. Monte Carlo results and indicator values including percentage contribution of each species are presented. The values above the group numbers represent the cluster group membership (i.e. closed, intermediate and open canopy) and the total number of trees included in the analysis. IV = Indicator Value (100 = perfect indication).

Canopy openness:	Closed [n=13]	Intermediate [n=9]	Open [n=11]				
Species	**Group 1 (%)**	**Group 3 (%)**	**Group 2 (%)**	**IV**	**Mean**	**StD**	**P-value**
Elaphoglossum petiolatum	71	0	0	71.4	23.8	7.91	0.000
Melpomene xiphopteroides	70	2	3	69.9	30.2	8.39	0.001
Pleopeltis mexicana	57	1	0	57.4	23.8	8.55	0.002
Tillandsia multicaulis	52	7	9	51.9	32.1	7.4	0.017
Stelis immersa	46	0	0	46.2	16.3	7.29	0.004
Pleurothallis matudana	44	0	4	43.8	22.4	7.77	0.020
Sphyrospermum cordifolium	40	8	0	39.8	22.8	8.05	0.046
Peperomia sp. 1	38	0	0	38.5	14.4	6.75	0.013
Stelis sp. 1	37	0	0	37.2	16.5	7.22	0.018
Werauhia werckleana	20	53	19	52.7	37.7	4.77	0.005
Tillandsia vicentina	8	56	24	56.2	38.2	6.6	0.015
Stelis villosa	2	12	46	45.8	29.2	8.59	0.049
Nephrolepis cordifolia	0	31	1	31	15.2	7.19	0.046
Encyclia tuerckheimii	0	0	27	27.3	11.8	6.54	0.048

4.4 Discussion

Studies that investigated hurricane effects on dependent plants have mostly been descriptive in scope (Loope et al. 1994), are commonly limited to a particular group of dependent plants (e.g. holo-epiphytes), limited to a particular section within the canopy (Goode and Allen 2008) and/or are restricted to only one disturbance event (Rodriguez-Robles et al. 1990, Mújica et al. 2013). Here we investigated how the community composition and diversity of 214 vascular dependent plants, sampled along the whole vertical forest profile, changed in relation to past hurricane impacts and to different environmental and structural variables.

Previous studies have suggested that dependent plant composition on a landscape level is mainly driven by differences in plot elevation (Frahm and Gradstein 1991, Wolf 1993, Hietz and Hietz-Seifert 1995, Kessler 2000), climate (Benzing 1998), aspect and exposure level. On a local level, on the other hand, characteristics such as host and stand properties and geographical distance between the host trees are often more important (Wolf et al. 2009). We therefore investigated the dependent plant communities between plots and trees separately. Our study found that 44.4% of the community dissimilarity at a plot level could be explained by elevation, VPD, aspect and exposure. The strongest vegetation clustering was observed between low and high elevation sites and among plots located near Base Camp and the Guanales camp site. Following the division between low and high elevation sites, 30% (as opposed to 7% prior to the division) of the dependent plant community dissimilarity at individual tree level could be explained by tree-specific environmental and structural variables. This is significantly more than reported from other studies (Wolf et al. 2009).

As many dependent plants are sensitive to changes in the meso- and microclimate (Benzing 1990), the decrease in VPD with higher elevation (see Chapter 3) has resulted in a clear separation of dependent communities at low and high elevation sites. Low elevation sites were represented by indicators such as *Jacquiniella teretifolia* [common colonizer of secondary vegetation and open canopies; Scheffknecht et al. (2010), Hietz et al. (2006) and Winkler

(2005)], *Tillandsia butzii* [drought resistant; Wolf (2005)] and *Serpocaulon triseriale* [found in drought-prone forests; Quaresma and Jardim (2014)]. High-elevation sites on the other hand were represented, amongst others, by species such as *Serpocaulon lasiopus, Tillandsia guatemalensis* [a mesic epiphyte; Castro Hernández et al. (1999)], *Tillandsia lampropoda* [occurs often in pine-oak dominated forest; Wolf and Flamenco-S. (2006)], *Tillandsia vicentina* [occurs often in higher elevation pine-oak forest; Wolf and Konings (2001)], *Werauhia werckleana* [indicator of mid- and late succession forest; Cascante-Marín et al. (2006)] and *Macleania insignis* [mesic and primarily found in moist conditions (Standley and Steyermark 1946)].

At a tree level, across the low and high elevation sites, mechanically dependent plants responded strongly to hurricane impact, canopy openness and different host trees (i.e. angiosperms versus conifers; Table A4.2 and Table A4.4). As mentioned previously, dependent plants can respond to hurricane damage directly and/or indirectly (Figure 4.9). Direct responses refer to damage to the dependent plant that can result in direct shifts in the dependent plant community. Indirect responses refer to effects at a community level that are influenced by the host/forest response to disturbance. There are two pathways related to indirect responses (Figure 4.9). Pathway one assumes that the host trees grow in frequently disturbed sites (e.g. frequent hurricane occurrence). This would result in a competitive advantage of some host trees over others. The resulting shift in host composition and the associated alteration in forest canopy structure will ultimately affect the canopy microclimate and the associated dependent plant community. Pathway two assumes that host trees grow in less frequently disturbed sites. The sudden responses of host trees to hurricanes (e.g. in creating a more open canopy) will be dependent on the tree damage probability of the individual (e.g. wood density) and of the stand.

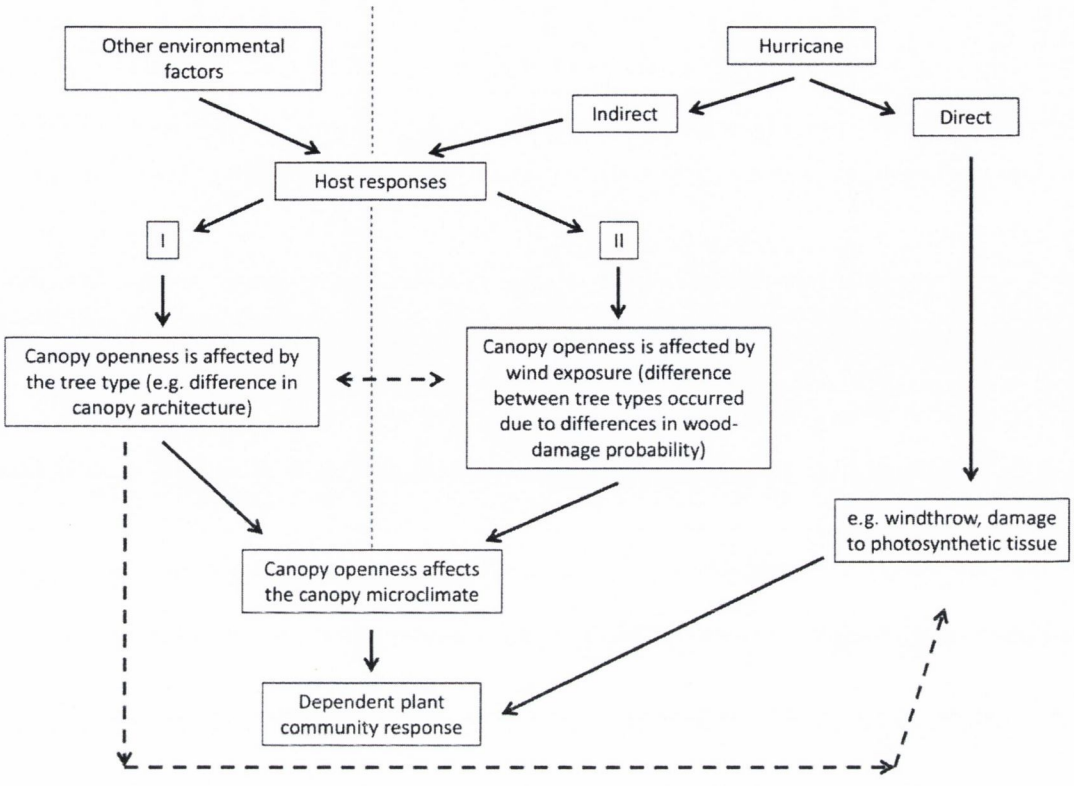


Figure 4.9 Direct and indirect mechanically dependent plant response-pathway to hurricanes. See text for more detail.

Pinus spp. had a more open canopy compared to angiosperm trees and were associated with disturbed sites (*pers. obs.* by the authors). Intuitively this could suggest that *Pinus* spp. in CNP were indicators of high disturbance sites. Evidence of this was observed following a landslide west of Cantiles from hurricane Mitch in 1998 and the subsequent dominance of *Pinus* spp. (*pers. obs.* by the authors). However, due to the higher vulnerability to damage of many fast-growing and shade-intolerant softwood species (Rich et al. 2007) (Chapter 3), one might expect that conifer trees become less dominant at these sites (Martin et al. 2007). One possible explanation for the observed association of *Pinus* spp. with disturbed sites could be that the frequency and intensity of hurricanes in the past has been relatively low (Chapter 2 and 3); the damage to *Pinus* spp. would not be strong enough to shift the community to an angiosperm dominated community. However, the damage to the forest would still be significant enough to allow pioneer species to colonize and become dominant

(Foster and Boose 1992). If this were the case, the increase in canopy openness and the resulting decline in dependent plant diversity and richness between the two tree types (*Pinus* spp. versus angiosperms) could be attributed to the damage probability of the tree species (Xi et al. 2008) (see Chapter 3). Dependent plants on fast-growing and shade-intolerant trees are therefore more vulnerable to hurricane damage due to their host's wood properties. This is only speculative however, and requires further investigation.

In addition, anthropogenic disturbances such as logging and shifting agriculture could have resulted in further alteration of the forest vegetation (González-Espinosa et al. 2006). The plots that were located near Base Camp and Guanales are more likely to have experienced greater anthropogenic pressures compared to plots that were located near Cantiles (*pers. obs.* by the authors). For example, *Pinus tecunumanii* (compared to *P. maximinoi*) has more frequently been observed in low elevation sites and secondary vegetation stands and has been less frequently recorded in mixed forest stands [D.L. Kelly *pers. obs.*; but see Galindo-Jaimes et al. (2002)]. Current deforestation rates in CNP are relatively high and 8.9 km^2 of forest has been lost since 2000 (0.4% per year). Most loss was reported from the NW site of the park (Neil Reid, Queen's University Belfast, *unpub.* data 2014). Prior to 2000, only limited evidence is available, but it is clear that considerable patches of forest surrounding Base Camp were heavily logged during the 1940's – 50's (Brown 1996). This was the site of a sawmill, and the remains of associated equipment can still be seen around the area and by the network of forest roads that radiate from there (most are now more or less abandoned; *pers. obs.* by the authors). Nevertheless, the extent to which logging events have impacted on the tree composition in CNP remains uncertain.

We detected significant diversity and compositional effects on mechanically dependent plant species along an impact gradient of past hurricanes. Across the elevation range, dependent plant diversity and species richness was negatively correlated with increased predicted past hurricane impact and canopy openness. Moreover, the dependent plant species composition was

strongly differentiated between the low impact (EVSS 1) and high impact (EVSS 5) sites along the damage gradient.

Open canopies can increase stress to the dependent plants through maximizing wind, sun and drought exposure and thus reducing favorable conditions for growth and survival (Zotz and Hietz 2001). More open canopies as a result of wind damage can result in direct community responses (e.g. increased mortality) or indirect community responses (e.g. changes affecting germination and establishment rates). This was demonstrated by Kartzinel et al. (2013), who found that canopy openness was strongly negatively associated with germination rates in Neotropical orchids. This was because disturbed sites did not provide favorable microsites for the epiphyte and the associated mycorrhizal community.

Mechanically dependent plants often have particular micro-site preferences within the forest canopy (Chapter 5), making them more or less likely to be affected by hurricane winds. Dependent plants for example, that grow on thinner or more exposed branches might be more vulnerable to damage and/or have evolved particular adaptations that enable them to survive strong winds. Hietz et al. (2002) pointed out that, for example, epiphytes that grow on more exposed and thinner branches achieve maturity much faster than other species. We were unable to detect any hurricane-related differences in dependent plant abundance and richness among branches of different circumference classes. This could be due to sampling bias, however, as we only sampled branches that had dependent plants present and because a higher proportion of the sampled branches were in the smaller branch size ranges. As baseline data of dependent plant occurrence was absent, the inclusion of branches that were free of dependent plants would still not have been sufficient to infer hurricane related incidences. The lack of dependent plants on such branches could simply reflect unfavorable conditions for establishment or sites that have not yet been exploited by dependent species (Chapter 5). This is not unlikely, as the establishment of dependent plants such as epiphytes is known to be slow (Nadkarni 2000) and is dependent on the species' dispersal mechanisms (Dassler and Farrar 2001, Cascante-Marín et al. 2009).

The slow recovery of dependent plant communities [high juvenile mortality (Werner and Gradstein 2008); slow growth rate (Laube and Zotz 2003); and slowness to reach maturity (Zotz 1995, Schmidt and Zotz 2002)], taken together with the recovery response of the forest to a relatively low frequency of recurring hurricane events (Chapter 2), have combined to produce a patchy disturbance mosaic within the forest. A similar picture was obtained for cypress (*Taxodium*) swamp forest in Florida (Oberbauer et al. 1996). Loope et al. (1994) reported that vascular epiphytes suffered the highest mortality rates of all plant groups (approximately 90% mortality) in upland and swamp forest in Florida following hurricane Andrew in 1992. They also noted that the epiphyte response to the hurricane damage varied among epiphytic groups, which resulted in an asymmetrical community response. For example, many *Tillandsia* species suffered significant sun damage compared to other groups such as orchids, which seemed less sensitive to increased solar radiation. In another study, Goode and Allen (2008) found that the epiphyte abundance was significantly reduced in a dry forest in Mexico following hurricane Wilma in 2005; the epiphyte species composition remained, however, similar to pre-hurricane conditions.

Most of the different life-forms in our study were correlated weakly to increased hurricane impact with minor changes in abundance and richness. Only holo- and hemi-epiphyte richness were significantly affected. As most of the dependent flora was comprised of holo- and hemi-epiphytes, most likely as our research design was less adequate for large individuals, this result was not unexpected. Closer investigation revealed that the decrease in richness was associated with particular species within life-form groups, rather than with particular life-form categories per-se. For example, species of the holo-epiphyte family Orchidaceae showed positive responses to increased hurricane impact; whereas many fern species showed negative responses (see Chapter 5 for more detail). As discussed by Loope et al. (1994), the increase in orchid richness is most likely the result of higher light radiation, probably as a result of increased canopy openness. Although orchids are very susceptible to hurricane damage (Rodriguez-Robles et al. 1990), particularly after the direct passing of hurricane winds (Migenis and Ackerman 1993), they are often superior to other

epiphytes in tolerating long desiccation periods [e.g. they have the ability to store water in most parts of their body (Ng and Hew 2000)]. Hemi-epiphytes and nomadic vines from the families Clusiaceae and Araceae have been shown to vary in their survival rates following experimental damage to their tissues (Patino et al. 1999).

The indicator species that were associated with different levels of hurricane exposure in our study varied between the two elevation sites. At low elevation sites, many mesic epiphyte species were associated with low hurricane impact. These included, amongst others, the orchids *Dinema polybulbon and Pleurothallis matudana,* the nomadic vine *Syngonium podophyllum* and two species of *Elaphoglossum* (fern). At high hurricane impact sites, the bromeliad *Tillandsia seleriana* was the most dominant indicator species. Interestingly, *T. seleriana* was also a good indicator for conifer trees and is often a disturbance-tolerant species (Wolf and Flamenco-S. 2006). At high-elevation sites, on the other hand, the orchids *Epidendrum ramosum* and *Rhynchostele cordata* were more associated with very high hurricane exposure sites and the ferns *Elaphoglossum petiolatum and Pleopeltis mexicana*, the bromeliad *Tillandsia multicaulis* and the epiphytic *Peperomia* sp. with low hurricane exposure sites. Not surprisingly, dependent plant species that were associated with low hurricane exposure were also strongly associated with closed canopies. This strongly suggests that past hurricane impact has indeed affected the forest canopy and resulted in a shift in dependent plant species composition along a gradient of hurricane impact. Although the community effect was clearly evident when comparing very high and very low impact sites, intermediate impacted sites were less distinct. This may reflect the recovery response of the forest, as high impacted sites would take longer to recover. Additionally, other factors (e.g. bark texture and the presence/absence of non-vascular epiphytes - see Chapter 5 for more detail) are also important species community composition drivers that could further help to explain the relatively low contribution of environmental variables (44.4% at a plot and 30% at a tree level) to the observed community dissimilarity in the ordination space.

In conclusion, dependent plant communities in CNP have been affected by the impact of past hurricanes. Direct effects were not observed, as the time-lapse between the fieldwork (2012-2013) and the last major hurricane impact (1998; Chapter 2) was too great. Both species diversity and composition indicated indirect effects derived from hurricane damage. The observed community shift, and the lower observed diversity of dependent plants with increasing hurricane impact, can most likely be attributed to structural and microenvironmental alteration of the forest canopy (e.g. branch breakage; see Chapter 3 for more detail). Several studies that have investigated structural and micro-environmental canopy alterations (e.g. due to logging) have demonstrated that dependent plant communities will change in response to these modifications. For example, Werner and Gradstein (2009) showed that epiphytes were ultimately constrained by changes in the canopy microclimate along a human disturbance gradient and that these changes were the result of structural alterations of the forest (e.g. canopy openness and increased edge effects). The dependent plant response we observed at CNP is much more noticeable at an individual species level than on a life-form level; this reflects the fact that eco-physiological responses can be highly variable even between ecologically closely linked taxa (Saldaña et al. 2005).

Direct effects on mechanically dependent plants (e.g. wind-throw and tissue damage) can mostly be measured only directly after the passing of hurricane winds, whereas indirect effects due to structural and microclimatic alterations of the forest canopy are more likely to be measureable for much longer. In regions where hurricanes activity is more frequent, dependent plant-community effects are likely to be much stronger. It has been shown that this can result in a long-term decline in mechanically dependent diversity (Mújica et al. 2013). Management and conservation efforts in relation to post-hurricanes dependent plant communities therefore need to focus on the identification of suitable host trees that have not been damaged by the hurricane winds and possibly the translocation of threatened species from disturbed areas to more suitable sites (Tremblay 2008). As in the case of CNP, forest conservation should not only consider the protection of primary forest sites but also incorporate sites that are less likely to be affected by hurricane storms. These sites can act as refuges for

dependent plants and increase the rates of recolonization following hurricane damage (Löbel et al. 2006). This could be particularly important in CNP, where many dependent plants appear to be very scare and/or very patchy in their distribution.

Chapter 5

Mechanically dependent plants and their response to different branch characteristics along a gradient of hurricane impact

5.0. Abstract

Different structural and environmental factors are known to be responsible for the distribution and abundance of mechanically dependent plants across the forest canopy. Here we investigated how 214 different dependent plant species from different life-forms, across 60 large canopy trees, responded to different structural and environmental canopy conditions in Cusuco National Park, Honduras. We also tested how dependent plants along individual branches responded to different levels of hurricane impact. A previously developed hurricane model was used that allowed us to identify trees in the study area that had been predicted to have differently been impacted by hurricanes over a 15-y period. The hurricane impact results were used to compare dependent plant abundance and richness along individual branches and across the canopy. We found that different life-forms showed strong vertical stratification. The total abundance of dependent plants was highest in the lower canopy, on sites that had been least impacted by hurricanes and highest in the upper canopy, on sites that had been most impacted by hurricanes. The shift in abundance along a gradient of hurricane impact resulted from a combination of abundance shifts of individual species and changes in the composition of dependent plants across sites. Mechanically dependent plant abundance and richness also correlated to different structural and environmental conditions along individual branches. The most important variables that explained most of the richness and abundance differences of life-forms and families among branches were: branch surface area, the presence of bryophytes, the absence of lichens and to a lesser extent differences in bark characteristics. We highlighted the importance of different environmental and structural variables on the distribution and composition of mechanically dependent plants and in relation to past hurricane impact.

5.1. Introduction

The position and distribution of mechanically dependent plants within the forest canopy is most likely determined at an early stage during establishment of seedlings (Zotz 1997). Different structural and environmental factors have been recognized to be limiting to the dependent plants' establishment and long-term persistence. These include (i) the location of the branch within the canopy along the vertical and horizontal canopy planes [reflecting microclimate conditions and resource availability: Graham and Andrade (2004); Griffiths and Maxwell (1999)]; (ii) the size of the establishment site [can increase habitat heterogeneity and prolong time for colonization (Zotz and Vollrath 2003, Laube and Zotz 2006)] and (iii) structural qualities (Wyse and Burns 2011), chemical [e.g. Valencia-Díaz et al. (2010) - but see Harshani et al. (2014)] and water-holding qualities of the bark (Callaway et al. 2002). Other important factors include (iv) the presence/absence of other dependent plants (Winkler et al. 2005); (v) disturbance dynamics within the forest (Nöske et al. 2008); (vi) time of establishment (e.g. season) and (vii) the branch distance to the nearest seed source (Mondragon et al. 2006). These interacting factors create complex multidimensional gradients that are exploited differently by different dependent plant species. As dependent plants vary in their ecological and physiological responses to these gradients, these factors would encourage niche differentiation along the vertical and horizontal plane (Freiberg 1997, Hietz and Briones 1998, Zotz and Hietz 2001). The quality of the establishment site can those determine the success of the individual.

Previous studies have reported particular location preferences of certain mechanically dependent life-forms, families and species across the forest canopy (ter Steege and Cornelissen 1989, Nieder et al. 2000, Zapfack and Engwald 2008). For example, species that are sensitive to drought conditions are more likely to be found in the interior and the lower canopy, where relative humidity is high and photon flux density is low (Benzing 1995). As dependent plants (with the exception of some climbing species) are essentially constrained to their germination site, strategies that allow them to tolerate (as opposed to avoid) particular structural and environmental conditions are more commonly shown [e.g. changes in leaf anatomy, type of photosynthetic pathway (e.g. C4),

adjustment of diffusive conductance and osmotic regulation]. However, sudden and/or large changes in the canopy environment (e.g. gap formation) would significantly reduce the effectiveness of particular tolerating adaptations. The dependent plant community is therefore expected to shift as a result of such changes.

One of the most dramatic structural impacts to forest canopies is the dislodgement of branches due to wind. Strong winds, from hurricanes in particular, can result in significant structural, microclimatic and biotic alterations in the canopy (Boucher et al. 1990, Oberbauer et al. 1996, Turton and Siegenthaler 2004, Turton 2013). This was demonstrated during previous work (Chapter 4), where we established that dependent plants responded, with regards to diversity and composition, to past hurricane events along different exposure levels in Cusuco National Park, Honduras. We also found that the microclimate along the vertical forest profile changed as a result of hurricane damage (Chapter 3). The structural and environmental changes in the forest canopy, as a result of storm damage, are therefore expected to affect the distribution of dependent plants along both vertical and horizontal planes.

The aims of this study are to identify structural and environmental variables that affect the dependent plant community composition and location preferences within individual host trees. It was predicted that dependent plant species, families and life-forms will vary in their abundance and richness along both vertical and horizontal planes. Any differences in their abundance, richness, composition and distribution will be the result of different structural and environmental branch characteristics. Moreover, we predicted that the abundance of dependent plants on individual branches and across the canopy will have changed as a result of the impact of past hurricanes. To test the latter, we used a hurricane model that was developed for Cusuco National Park, Honduras, which allowed us to identify sites that had varied levels of predicted hurricane damage over a 15-y period (1995-2010). See Chapters 2, 3 and 4 for more detail.

5.2. Methodology

5.2.1. Tree and plot selection

See Chapters 2, 3 and 4 for further detail.

5.2.2. Within-tree data collection

As described in Chapter 4, every branch that hosted vascular mechanically dependent plants was sampled. At an individual tree level we recorded branch characteristics such as length and circumference of each branch, bark texture, aspect and inclination. The length and circumference of the branch was used to calculate total branch surface area as described by Batke (2012). The branch texture was classed according to the degree of roughness, fissuring and flakiness. Each category was independently scored by two observers as being absent, weakly developed or strongly developed (score 1-3). The aspect and inclination of each branch was measured using a standard compass with clinometer. Aspect was measured by following the general situation of each branch. Branches that had unusual growth forms (e.g. zigzag growth) were divided into multiple sections and each section recorded individually for aspect. In addition to vascular dependent plant abundance, bryophyte cover and lichen cover were estimated for each branch (and bole), using a 0-100% scale with 5% intervals.

The position of each dependent plant or clonal patch of dependent plants was recorded by measuring the height of the individual/patch to the ground and the mean distance of each dependent species/patch to the centre of the tree. The local position of each dependent plant individual was recorded by dividing the branch into six sections. The first partition was between the adaxial side (i.e. top of the branch) and abaxial side. The fork, lower-, mid- and upper-third of the branch formed the remaining subdivisions. The fork was defined by measuring a 10 cm radius from the bifurcation point. Any dependent plants that were rooted within this space were classed as having occurred within the fork. The locations of hemi-epiphytes, climbers, nomadic vines and mistletoes were measured by identifying as far as possible the position of the initial rooting point and by measuring their total height and the cardinal aspects of the individual relative to the centre of each tree. For climbers for which it was not possible to

determine a germination point, we estimated the total area they occupied and recorded the aspects they covered on the tree (see Chapter 4 for the different life-form classifications).

Finally, microclimate measurements were recorded from 20 of the 60 tress. Data loggers were suspended in individual trees and along the vertical canopy at set intervals. The loggers measured relative air humidity and temperature over a 12-month period (see Chapter 3 for more detail).

5.2.3. Hurricane model

See Chapters 2, 3 and 4 for more detail.

5.2.4. Data analysis

Throughout the analysis, branches were treated as individual sampling units. To identify the vertical and horizontal distribution of dependent plants, we correlated structural and environmental variables to dependent plant richness and abundance at a life-form, family and species level using Linear Models (LM), Linear Mixed Models (LMM), Spearman's Rank coefficient and Analysis of Variance (ANOVA). To test the frequency distribution of dependent plant families and species between different branch divisions a G-test with a Williams correction factor was used (Dytham 2003). The G-test is based on the specific multinomial distribution as opposed to the approximate multinomial distribution of a chi-squared test. The test was run in 'R' using a script provided by Hurd (2012). The G-test was run at a dependent plant family and species level for each branch division. Nomadic vines and climbers were not included in this analysis as they often covered multiple branches at a time.

To assess how different environmental variables contributed to the community structure of dependent plant families and life-forms among different branches, NMS ordinations were used (see Chapter 4 for more detail). Environmental and structural variables that were used in the second matrix included branch surface area, inclination, aspect, bark characteristics (i.e. roughness, fissuring and flakiness) and bryophyte and lichen cover. Branch inclination was divided into three classes after Ingram and Nadkarni (1993): angle class one comprised branches between 0-30°, angle class two branches between 31-60° and angle

class three branches between 61-90°. Additionally, we used a Morisita index of dispersion (MID) to identify the degree of aggregation of dependent plant species, life-forms and families (Arevalo and Betancur 2006). The MID was defined by Morisita (1962) and describes the spatial pattern of individuals in a population. It is calculated as follows:

$$I_p = \frac{n\left(\sum x_i^2 - \sum x_i\right)}{\sum x_i^2 - \sum x_i} \qquad \text{(Eq. 5.1)}$$

Where x_i is the count of individuals in sample *i* and *n* is the number of samples. The index falls between 0 and *n*. A value of one indicates a random dispersion, a value of < 1 indicates a uniform dispersion and value of > 1 indicates a clumped dispersion. The values were recalculated using 95 percent confidence limits following Smith-Gill (1975) and by removing all singleton species. A chi-squared test was used to identify values that were significantly different from one.

In previous chapters (Chapters 2, 3 and 4) we correlated hurricane impact scores derived from a model to tree damage, microclimate and dependent plant composition data, in order to identify structural and microclimate differences between trees that had been impacted differently by past hurricanes. The same model was used in this chapter, in order to compare dependent plant diversity among branches that were located across trees of different degrees of hurricane exposure. We correlated the best-fit model solution (i.e. the south model solution) to dependent plant diversity data along individual branches. Each branch was treated as an individual sampling unit.

All calculations were done in PC-ORD 6 (McCune and Mefford 2011), DataDesk (Velleman and John 1996) and 'R' (R Developing Core Team 2011).

5.3. Results

5.3.1. Host characteristics

See Chapter 4 for more details on the different host trees.

5.3.2. Dependent plant location along the branch

A total of 1188 branches were sampled, with an average of 4.1 vascular dependent plant species per branch (max. = 14 and min. = 1). Total species richness of all dependent flora was 214 (see Chapter 4 for more detail). At a species and family level, dependent plants showed significant branch location preferences for the adaxial or abaxial sides of the branch (Table 5.1). However, no significant preferences were detected among the forks and the lower-, mid- and upper-third of the branches (Table 5.1).

Table 5.1 G-test results with Williams correction, testing how dependent plant species (holo- and hemi-epiphytes only) and families differed in their growth location preferences along individual branches.

		G-value	DF	P-value
Adaxial vs. Abaxial				
	Family	158.34	68	<0.001
	Species	688.58	338	<0.001
Fork vs. Lower vs. Mid vs. Upper				
	Family	30.45	476	>0.05
	Species	77.36	2366	>0.05

Of the 6870 individual holo- and hemi-epiphytes investigated, 69% were found only on the adaxial side of the branch and 27% were found only on the abaxial. No statistical difference in the dependent plant location preference (adaxial versus abaxial) was found between angiosperm and conifer trees ($P > 0.05$). At a family level, most individuals of the Bromeliaceae were found at the adaxial side of the branch (62%) compared to the only 34% on the abaxial side. The remaining 4% were shared between the two sides. Most Orchidaceae individuals occupied the adaxial side of the branch (84%) and only 13% occupied the abaxial side, with a 3% overlap between the abaxial and adaxial sides. Again, most Pteridophytes (ferns and clubmosses) occupied the adaxial sides of the branch (62%), with 34% occupying the abaxial side. Although not significant (Table 5.1), over one third of dependent plant individuals (33%) were only found in the mid-third of the branch, 22% on the lower third, 20% at the

upper third and 6% in branch forks. The remaining 19% occupied a combination of these locations. The only species that was found more frequently in branch bifurcation points than expected by chance was the tank bromeliad *Werauhia werckleana* (Mez) J.R. Grant.

To test whether the abundance of holo-epiphytes on the adaxial and abaxial surfaces of the branches were different along a gradient of hurricane impact, we used a G-test. Dependent plant abundance on the adaxial branch surface decreased with increasing hurricane incidence, however this was not significant at a community level ($G = 22.97$, $P > 0.05$). Moreover, there was no difference in abundance on the abaxial branch surface with increasing hurricane impact at a community level ($G = 41.1$, $P > 0.05$). At a family level, abundance did change with hurricane impact ($P < 0.01$). For example, Bromeliaceae abundance at low impact sites was highest both on adaxial branch surfaces (72.8%) and on abaxial branch surfaces (50.8%). Orchidaceae abundance showed a reversed pattern. On high impacted sites, orchid abundance was highest on the adaxial branch surfaces (89.9%) and lowest on the abaxial surfaces (10.2%).

5.3.3. Three dimensional arrangements

5.3.3.1. Species abundance

As the location of the dependent plant individuals along the branch (including the forks) does not necessarily present a true image of their proximity in the horizontal plane, we also measured the actual distance for each dependent plant (or epiphyte patch in clonal individuals) from the center of the tree. Dependent plant abundance with mean distance from the bole was significantly different among different dependent plant life-forms ($F_{4,242} = 22.27$, $P < 0.01$; Figure 5.1). Post-hoc Bonferroni correction and LM comparisons showed that this difference was mainly driven by holo-epiphytes ($t = 2.6$, $P < 0.01$) and mistletoes ($t = 3.9$, $P < 0.01$). Mistletoes and holo-epiphytes had higher abundances at the outer canopy compared to other life-forms (Figure 5.1).

Life-form abundance varied also in relation to height in the canopy ($F_{4,242} = 49.9$, $P < 0.01$; Figure 5.1). Holo-epiphytes had their highest abundance

between 20 and 30 m. Holo-epiphyte abundance was significantly different to nomadic vines and hemi-epiphytes ($P < 0.01$). Hemi-epiphytes had their highest abundance between 20-30 m and their abundance was significantly different from all other life-forms ($P < 0.01$) but not from holo-epiphytes ($P > 0.05$). Nomadic vine abundance was highest at the bole of the trees (0-10 m) and was significantly different from holo-epiphytes, climbers, hemi-epiphytes and mistletoes ($P < 0.01$). Mistletoe abundance was highest between 30 and 40 m and was not significantly different from most life-forms ($P > 0.05$), with the exception of accidental epiphytes and nomadic vines ($P < 0.01$). Finally, accidental epiphyte abundance was highest at the bole of the trees (0-10 m) and was significantly different from all dependent plants ($P < 0.01$), but not nomadic vines ($P > 0.05$). The families that contributed most to the observed differences in height pattern between different life-forms were Bromeliaceae (holo-epiphytes), Clusiaceae (primary hemi-epiphytes: *Clusia* spp.), Araceae (nomadic vines: *Anthurium* spp.), Passifloraceae (climbers: *Passiflora* spp.), Loranthaceae (mistletoes) and Lomariopsidaceae (accidental epiphytes: terrestrial fern) (Figure 5.1).

At life-form, family and species level, abundance did not change with height and distance when modeled as a function of these (life-form: $F = 0.19$, $P > 0.05$; family: $F = 0.29$, $P > 0.05$; species: $F = 0.79$, $P > 0.05$; Figure 5.2). This was because distance did not significantly contribute to the model performance ($P > 0.05$). Therefore, only height was important in explaining the dependent plant abundance distribution along the vertical and horizontal planes, in the absence of other structural and environmental variables.

To investigate whether dependent plant abundance changed with height in the canopy as a result of differences in tree species and physiognomic types (broadleaved angiosperms versus needle-leaved conifers; see Chapter 3 for more details), we used LLM models. The different models were validated using akaike information criterion (AIC). The best fit model suggested that including tree type ($t = 2.2$, $P < 0.05$), but not species ($P > 0.05$), did increase model performance. Abundance at a branch level increased with height as a result of tree type. Mean dependent plant abundance in conifer trees was higher at

branches that were located closer to the upper canopy. Post-hoc analysis showed that this difference reflected a lower canopy surface area between 40-60 m in angiosperms compared to conifer trees ($t = -3.7$, $P < 0.01$).

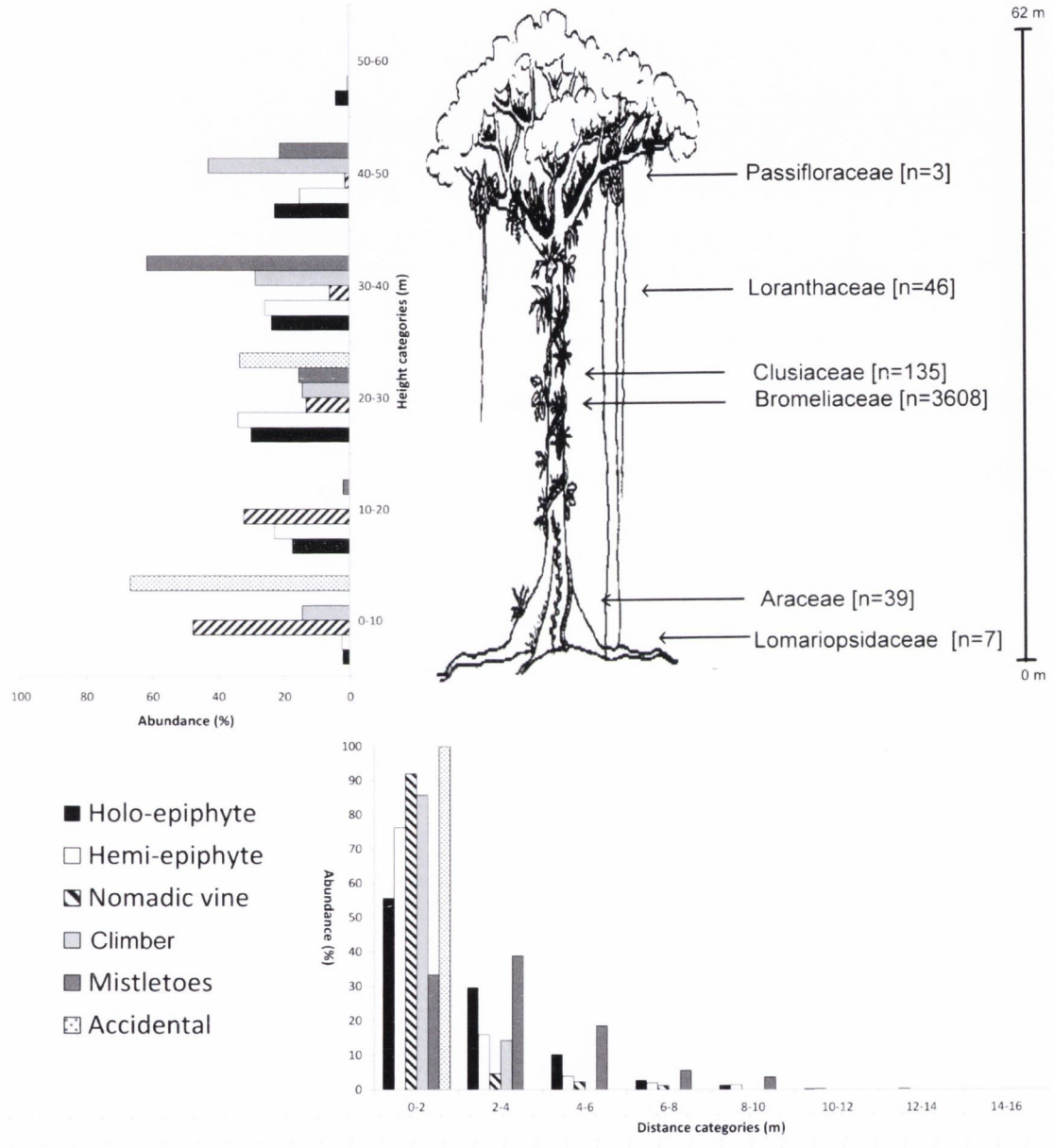


Figure 5.1 Percentage dependent plant abundance, with mean horizontal distance from the tree center and mean canopy height for the different life-forms. The families that contributed most to the observed height structure along the vertical canopy profile for each life-form are shown.

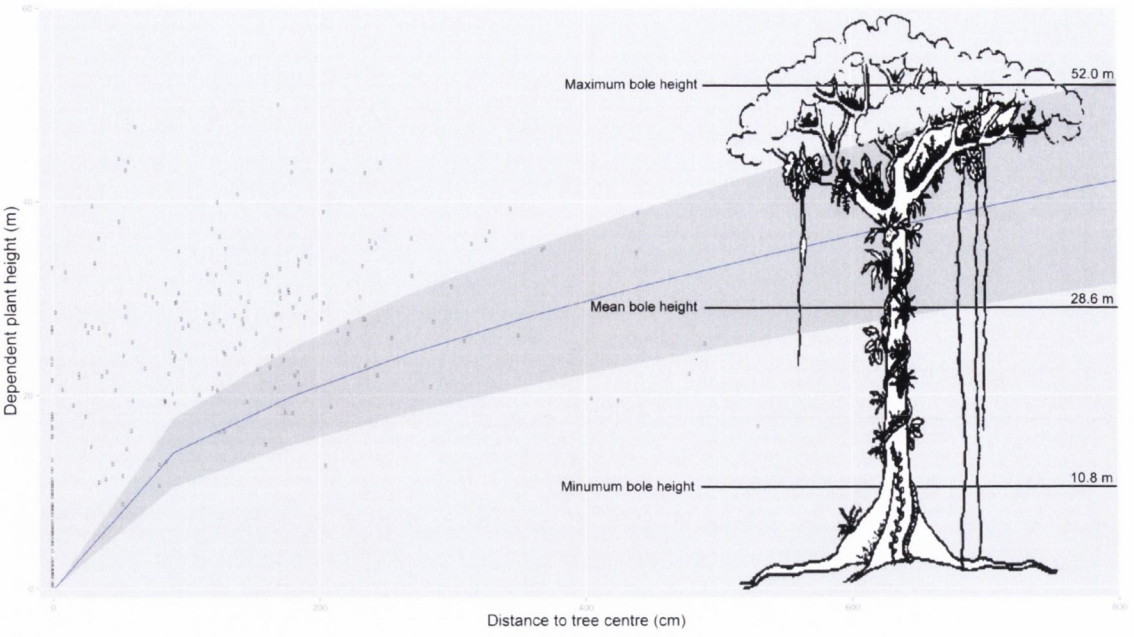


Figure 5.2 Distribution of dependent plant species with height in the canopy and distance to the tree center. Each dot represents a species. A LM of dependent plant abundance was superimposed as a function of mean dependent plant height and distance (blue line = LM; grey shade area = standard error). The mean, maximum and minimum bole heights are also given (right hand side).

We tested how mean dependent plant abundance changes with height in the tree and distance from the tree center along the gradient of hurricane impact. The abundance of dependent plant with distance to the tree center did not change with increased hurricane impact ($P > 0.05$). However, the relationship between dependent plant abundance and height in the tree varied in relation to hurricane impact level ($t = 2.02$, $R^2 = 0.1$, $P < 0.05$). Dependent plant abundance decreased with level of hurricane impact on a branch level (Figure 5.3 and Chapter 4). Abundance was highest on branches located on the lower parts of the tree in areas where hurricane impact was low, and lowest on branches located on the lower parts of the tree in areas where hurricane impact was high (Figure 5.3).

Following closer investigation it became apparent that the observed patterns in Figure 5.3 could be mainly attributed to an abundance shift of individual species. For example, *Tillandsia vicentina* Standl. (a bromeliad) abundance increased with increasing hurricane impact and the abundance shifted from the lower and middle canopy (20-40 m) to middle and upper canopy (40-60 m).

Furthermore, the drought resistant bromeliad *Tillandsia seleriana* Mez. was absent at very low and low impacted levels. The highest abundance of this species was observed at very high impacted levels, at the middle canopy (20-30 m). The abundance of the fern *Pleopeltis mexicana* (Fee) Mickel & Beitel was highest at branches located between 20-40 m in low impact levels; it was almost completely absent at medium, high and very high impacted levels. The tank bromeliads *Catopsis hahnii* Baker and *C. floribunda* L.B. Sm. were completely absent at very low impacted levels but increased towards high impacted levels. However, *C. hahnii* was absent at very high impacted levels. Most individuals were found between 40-60 m at medium impacted levels and between 40-50 m at high impacted levels. At very low impacted levels, the atmospheric bromeliad *Tillandsia butzii* Mez. was almost completely absent throughout the canopy. Abundance increased substantially with hurricane impact. At low impacted levels *T. butzii* abundance was highest at the middle and upper canopy (40-50 m); at high and very high impact levels the highest abundance shifted towards lower canopy branches (20-40 m). Finally, the abundance of the tank bromeliad *W. werckleana* was highest, across the different impact levels, in the lower canopy (0-20 m).

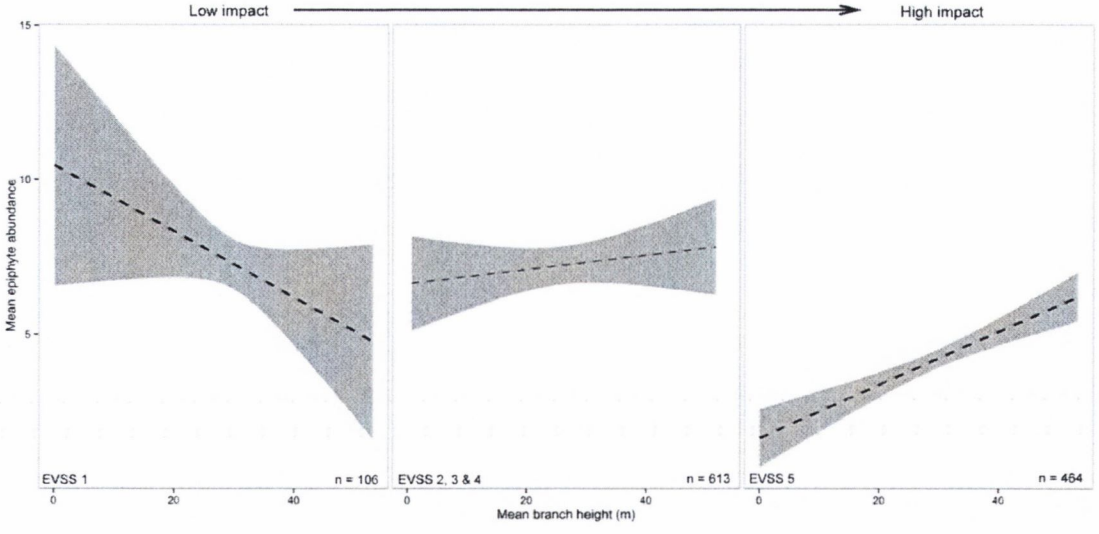


Figure 5.3 Mean dependent plant abundance correlated to mean branch height across the different hurricane impact levels. The dashed line represents the line of best-fit and the grey shaded areas are the 95 % confidence limits. The number of branches that were included in the analysis between the different impact levels is noted at the bottom

of each graph. Note that only a total of 60 branches were randomly selected for the final analysis.

5.3.3.2. Species richness

A polynomial regression was used to test how dependent plant richness changes along the vertical canopy profile. This regression type was used as the data visualization predicted a curvilinear relationship between richness and height within the tree. Richness was found to have changed curvilinearly with branch height ($df = 1172$, $F = 16.04$, $P < 0.01$). Richness increased with height in the canopy but decreased at approximately 35 m (not shown). However, richness did not increase with distance from the bole ($df = 1179$, $F = 3.9$, $P > 0.05$). Interestingly, the curvilinear increase in species richness with height did not correlate with the number of branches sampled at each height ($t = -1.17$, $P > 0.05$) but was positively correlated to branch surface area (Table 5.2). Branch surface area did not correlate with branch height ($df = 1179$, $F = 2.9$, $P > 0.05$), but the number of branches observed and species richness were positively correlated with branch surface area ($df = 1179$, $F = 4.94$, $P < 0.05$). In summary, a higher number of branches resulted in a higher surface area, which in return had a positive effect on species richness. However, branch surface area (for all tree species) in the mid and upper canopy did not change with increasing height, but species richness did.

To identify whether this difference in species richness with area was the result of differences between different tree species and tree life-forms (e.g. conifers versus angiosperms), mixed effect models were used. The different models were validated using AIC. The best fit model suggested that including tree species and life-forms did not increase model performance ($P > 0.05$). Thus, richness at a branch level did not increase with area and height as a result of tree species and life-forms (see also Chapter 4).

To identify how different environmental and structural variables were correlated with species richness a Spearman's Rank test was used (Table 5.2). Richness was positively correlated with bryophyte cover, bark roughness and bark fissuring. Richness was negatively correlated with lichen cover and bark flakiness. Branches with a higher surface area had significantly higher

bryophyte cover, lower lichen cover and rougher and more deeply fissured bark. Additionally, branches that had a steeper inclination had higher bryophyte and lichen covers (Table 5.2). Mean bryophyte cover was higher in angiosperm trees (38.2%) compared to conifer trees (17.2%, $P < 0.05$) but mean lichen cover did not differ between the two types (23.3% and 21.2% respectively, $P > 0.05$). Moreover, bryophyte cover was significantly lower on branches located in trees that were more impacted by hurricanes (EVSS 1 = 51.7%; EVSS 5 = 20.9%; $R^2 = 0.68$, $P < 0.01$).

Table 5.2 Spearman's Rank correlations between environmental and structural variables and species richness. Branches were treated as sampling units. Note that aspect was previously transformed (see Chapter 4). All significant values are given in bold (df = 1108).

	Surface area	Inclination	Aspect	Bryophyte cover	Lichen cover	Roughness	Fissuring	Flakiness	Species richness
Surface area	1								
Inclination	**0.15**	1							
Aspect	0.05	0.00	1						
Bryophyte cover	**0.11**	**0.10**	-0.01	1					
Lichen cover	**-0.12**	**0.21**	-0.01	**-0.15**	1				
Roughness	**0.24**	0.05	0.02	**0.17**	**0.16**	1			
Fissuring	**0.27**	**-0.11**	0.03	-0.05	0.02	**0.50**	1		
Flakiness	-0.04	**-0.16**	0.00	**-0.37**	**-0.24**	**-0.22**	**-0.10**	1	
Speices richness	**0.47**	**-0.13**	0.05	**0.29**	**-0.34**	**0.18**	**0.19**	**-0.12**	1

In a previous chapter we demonstrated that the microclimate along the vertical forest profile changed with height in the canopy but not between different tree life-forms (Chapter 3). However, because the data were based on only 20 of the 60 investigated trees, we were not able to correlate vascular dependent plant richness directly to microclimate variables. According to the data from the 20 trees, vascular dependent plant richness was negatively correlated with mean, maximum and minimum temperature ($R^2 = 0.1$, $P < 0.01$) and positively correlated with mean RH ($R^2 = 0.02$, $P < 0.01$), but not with maximum and minimum RH ($P > 0.05$). As the correlations were very weak, we were not able to make satisfactory predictions across all 60 trees. Therefore, we investigated whether we can use non-vascular epiphyte cover as a proxy for temperature and RH instead, as they showed significant correlations with vascular species richness (Table 5.2).

We correlated non-vascular epiphyte cover at a branch level with RH and temperature at each canopy position (i.e. the lower, middle and upper canopy; see Chapter 3). Bryophyte cover increased significantly with RH and decreased with temperature and lichen cover decreased significantly with RH and increased with temperature (Figure 5.4). Generally, RH and temperature were poor indicators of bryophyte and lichen cover, although lichen cover was a better microclimate predictor compared to bryophyte cover.

5.3.4. Community analysis

A NMS was used to identify different environmental variables that might have influenced the community composition between different branches, dependent plant families and life-forms. At a life-form levels three distinctive clusters were identified along the 2-dimensional model solution (stress value = 6.1; Figure 5.5). Sørensen (Bray-Curtis) distance measure revealed that axis one had the strongest correlation, followed by axis two (Table 5.3). The three identified cluster groups were significantly correlated with axis one but not with axis two (Table 5.3, Table A4.3). Branch surface area was the strongest environmental factor that was driving the grouping in the ordination space, followed by bryophyte and lichen cover, bark roughness, fissuring and flakiness (Table 5.3, Table A4.3 and Table A4.4). Cluster group one and two was mainly driven by branches that had a higher surface area and higher bryophyte cover, whereas cluster group three was mainly driven by the higher abundance of lichens.

Table 5.3 Branch dependent-plant NMS ordination axis scores correlated to environmental variables using Spearman's rank correlation coefficient. Individual branches were used as a sampling unit and two separate ordinations were run, at life-form and family levels. A Sørensen (Bray-Curtis) distance measure was used to identify the proportion of variance explained for each axis (R^2). Only coefficient values that were significant are shown ($P < 0.05$). df = 1108; ns = non-significant.

	Group membership	Surface area	Inclination	Aspect	Bryophyte cover	Lichen cover	Roughness	Fissuring	Flakiness
Life-form									
Axis1 (R^2 = 0.9)	0.46	-0.46	0.13	ns	-0.21	0.31	-0.19	-0.19	0.09
Axis2 (R^2 = 0.8)	ns	ns	ns	ns	-0.18	ns	ns	ns	0.16
Family									
Axis1 (R^2 = 0.4)		0.15	ns	ns	0.23	0.07	0.29	ns	-0.21
Axis2 (R^2 = 0.7)		0.39	-0.05	ns	0.34	-0.32	0.15	ns	-0.08
Axis3 (R^2 = 0.9)		-0.20	0.17	ns	0.24	ns	ns	-0.15	ns

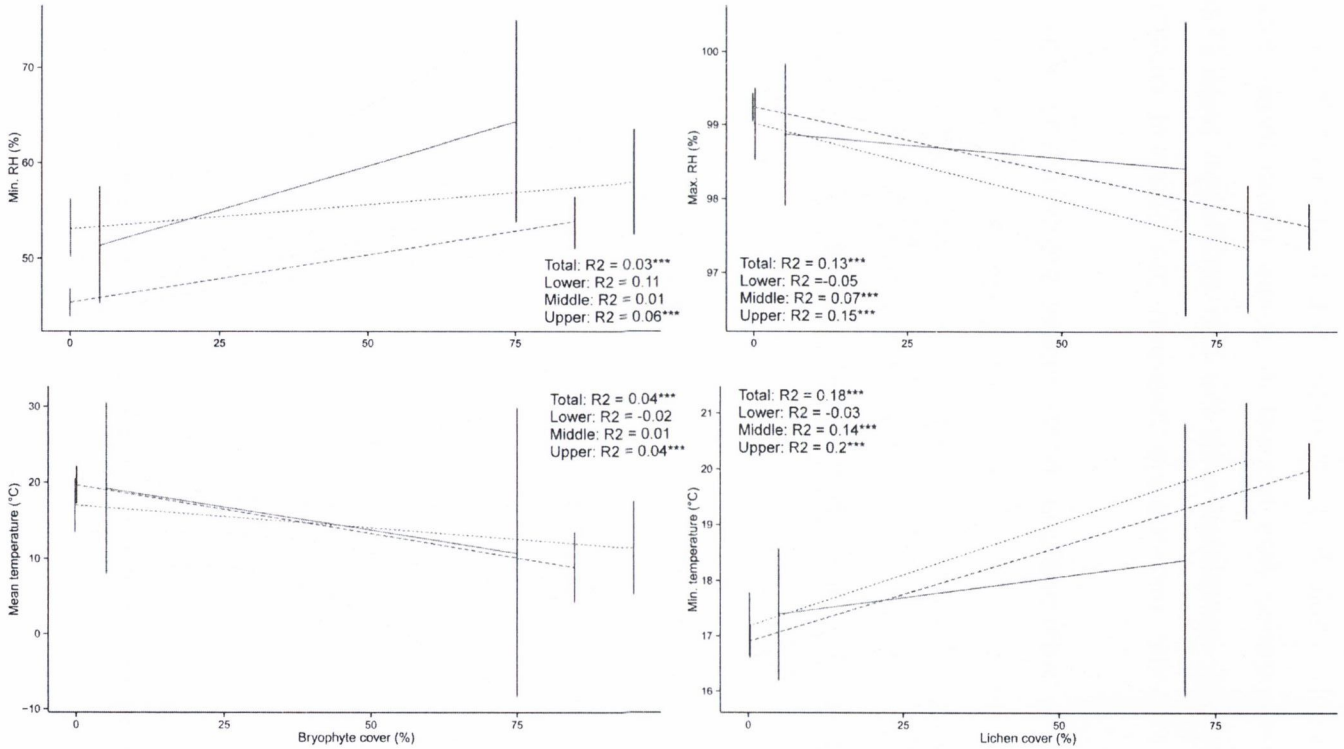


Figure 5.4 Relationships of relative air humidity (RH) and temperature with bryophyte and lichen cover on canopy branches at different canopy positions within 20 sample trees. The solid lines represent the linear fit for the lower canopy. The dotted lines represent the linear fit for the middle canopy and the dashed lines represent the linear fit for the upper canopy (***P < 0.01).

The abundance of different dependent life-forms changed along the ordination axis. Holo-epiphyte abundance was highest in cluster group one (Figure 5.6) and was strongly correlated to axis one (Table 5.4). Hemi-epiphyte abundance was highest in cluster groups one and two (Figure 5.6); however, this association was weak (Table 5.4). Nomadic-vine abundance in cluster group two and climber abundance was highest in cluster group three (Figure 5.6); they were both weakly correlated with the two ordination axes (Table 5.4). Mistletoe abundance did not change between the different cluster groups (Figure 5.6; Table 5.4).

At a family level, a 3-dimensional NMS model solution was recommended (stress value = 12.5). Sørensen (Bray-Curtis) distance measure revealed that axis three had the highest correlation between ordination distances, followed by axis two and axis one (Table 5.3, Table A4.3). As with the life-form community analysis, the most important environmental variables at a family level were lichen and bryophyte cover and branch surface area (Table 5.3). Orchidaceae was significantly correlated with axis one, whereas Bromeliaceae was correlated to axis two and three. Polypodiaceae was weakly correlated with axis two. Most other family-axis correlations were very weak (Table 5.4, Table A4.3). Finally, a Morisita index of dispersion (MID) at a community level (i.e. individual species), life-form and family level showed that the dependent plant community and the different life-forms were clumped in their distribution. At a family level, Clusiaceae (*Clusia* spp.) was the only taxonomic group that showed a uniform distribution pattern (Table 5.4). However, the sample size was very low for that family (Table 5.4).

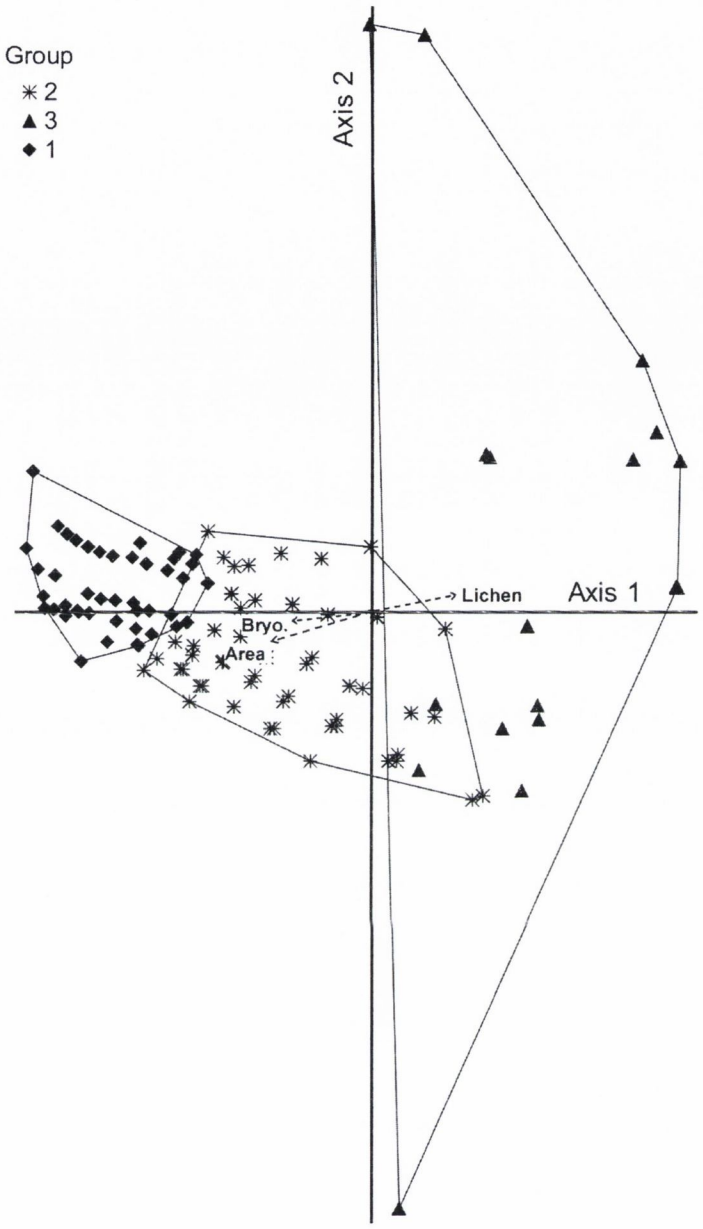


Figure 5.5 NMS ordination and joint plot with individual branches as sampling unit. The three cluster groups are indicated by different symbols.

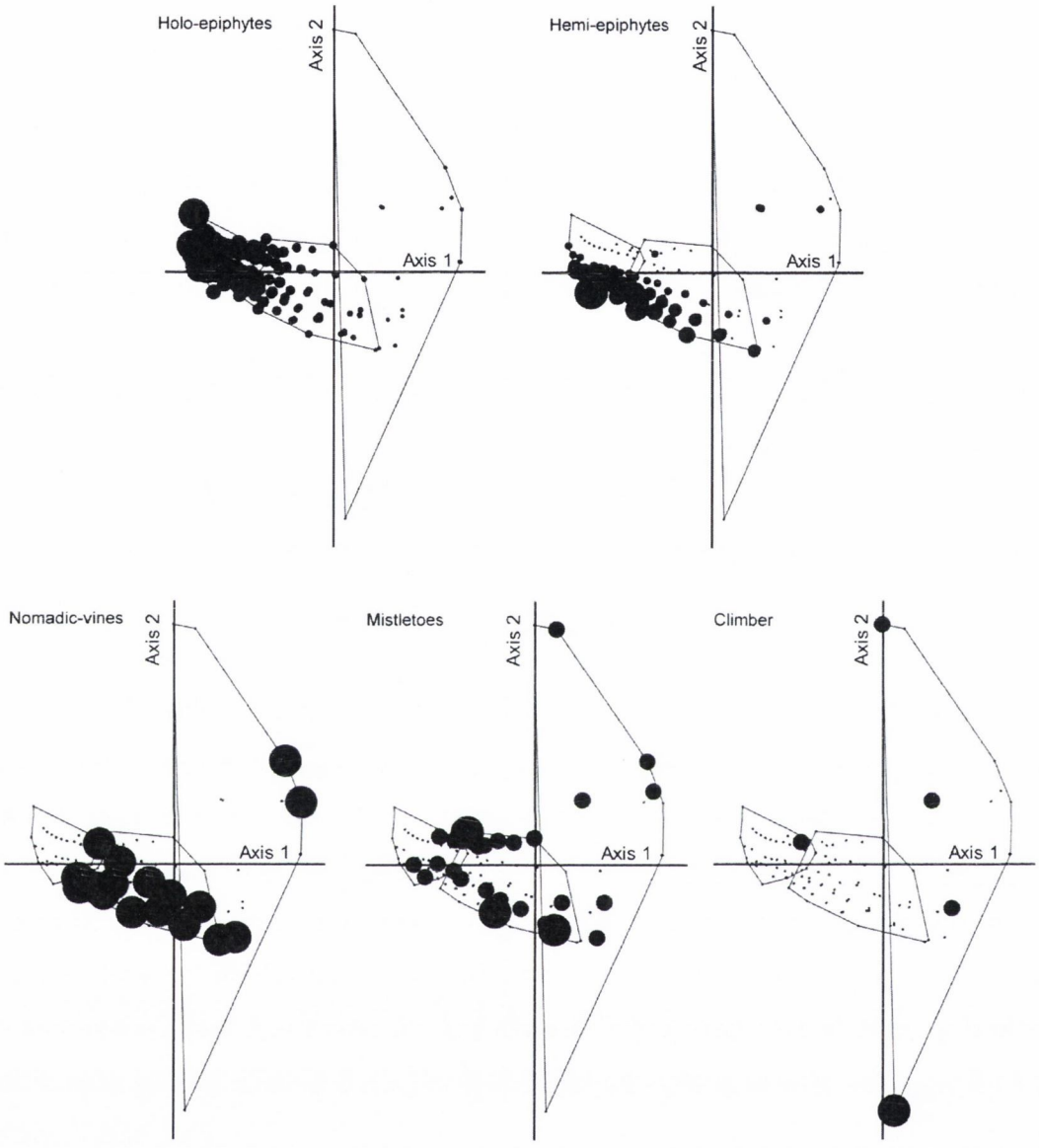


Figure 5.6 NMS ordinations of the five life-forms. The three cluster groups are indicated by solid lines. Each circle represents a branch and the size of the circle indicates the life-form abundance (large = high abundance).

Table 5.4 Tau and R^2 correlations between the different life-forms and the most important dependent plant families (i.e. number of species and abundance), for each identified NMS ordination axis. Additionally, the rescaled Morisita's standardized index of dispersion (I_p) for the whole community (i.e. individual species), each life-form and the most important families. Individual branches were treated as independent sample units. I*p* varies between -1 and +1 and will average I*p* = 0 for a random pattern.

		Axis1		Axis2		Axis3		Morisita (I_p)	Distribution pattern
Level		R^2	Tau	R^2	Tau	R^2	Tau		
Community:								0.24	Clumped
Life-form									
	Holo-epiphyte (n=123)	0.82	-0.94	0.01	0.19			0.50	Clumped
	Hemi-epiphyte (n=18)	0.13	-0.30	0.10	-0.37			0.50	Clumped
	Nomadic vine (n=19)	0.00	-0.02	0.01	-0.10			-0.12	Clumped
	Mistletoe (n=6)	0.00	-0.04	0.07	0.12			0.41	Clumped
	Climber (n=46)	0.00	0.01	0.01	0.02			0.52	Clumped
Family									
	Araceae (n=19)	0.00	0.01	0.01	0.07	0.01	0.07	0.50	Clumped
	Araliaceae (n=4)	0.00	0.00	0.02	0.10	0.00	0.01	0.50	Clumped
	Bromeliaceae (n=25)	0.17	-0.30	0.30	0.45	0.31	-0.46	0.50	Clumped
	Clusiaceae (n=4)	0.01	-0.07	0.15	0.31	0.00	-0.02	-0.78	Uniform
	Dryopteridaceae (n=8)	0.04	0.19	0.27	0.43	0.11	0.30	0.50	Clumped
	Ericaceae (n=5)	0.00	0.04	0.14	0.30	0.01	0.08	0.50	Clumped
	Orchidaceae (n=52)	0.52	0.67	0.03	0.10	0.10	-0.27	0.50	Clumped
	Polypodiaceae (n=26)	0.01	0.12	0.35	0.53	0.15	0.31	0.50	Clumped
	Vitaceae (n=5)	0.01	0.05	0.00	-0.01	0.00	0.01	0.51	Clumped

5.4. Discussion

5.4.1. Vertical stratification

As the upper and outer canopy are exposed to different microclimatic conditions from the lower and inner canopy (Thompson and Hinckley 1977, Chen et al. 1999, Zhang et al. 2013), we would expect to see dependent plant abundance and species richness patterns across the vertical and horizontal planes (Zotz and Vollrath 2002, Winkler et al. 2007). Interestingly, our results showed that the main difference in dependent plant abundance and richness was with height in the tree, not with distance from the tree centre. Species richness changed curvilinearly with height and was greatest at approximately 35 m (mean canopy height was 40.4 m). Dependent plant abundance varied with height between different epiphytic life-forms and families. For example, the nomadic vine aroid (Araceae) species (including *Monstera*, *Philodendron*, *Anthurium* and *Syngonium*), were mostly located on the tree bole. As pointed out by Ray (1992), many species in these genera have shoots that cannot support

themselves without structural support from other plants during upwards growth. As they often germinate at ground level, they have to migrate to favorable sites to mature (Ray 1992, Andrade and Mayo 2000). Moreover, many of these species prefer more shaded and humid conditions (Ray 1992, Zotz 2007), which are more prevalent in the lower canopy.

Parasitic mistletoe species from the family Loranthaceae were mainly found in the upper canopy. Mistletoes have a unique ecology with regards to their seed dispersal. Seeds are dispersed by animal vectors such as birds; the bird regurgitates or defecates the seed against the host substrate and the seeds sticks to the branch by means of viscous tissue (de Buen and Ornelas 2002). The high abundance of mistletoes in the upper canopy could therefore be a reflection of the perching preferences of the seed vector. Moreover, mistletoes have a higher germination rate on thin branches, branches that receive higher sunlight and are located in relatively warm conditions (Sargent 1995).

Holo- and hemi-epiphytes are more dependent on the structural area and support of the branch compared to other life-forms. This was reflected in the higher abundance of holo- and hemi-epiphytes on branches that were larger. As the total tree surface area in the middle and upper canopy did not change with height in the canopy, the high abundance of holo- and hemi-epiphytes between 20-30 m would therefore be more likely to reflect particular micro-environmental habitat characteristics along the vertical gradient. For example, the clumping of dependent plants along the horizontal gradient (Jian et al. 2013) may be related to irregular distribution of high quality resource sites across the canopy (Nieder et al. 2000) and the uneven dispersal of seeds within and amongst host trees (Burns and Zotz 2010).

Dependent plant abundance shifted along a gradient of hurricane impact. Overall, dependent plant abundance was highest in the lower canopy in areas where hurricane impact was low, and highest in the upper canopy in areas where hurricane impact was high. The shift in abundance with increasing hurricane impact was mainly a reflection of abundance changes among individual species but was compounded by compositional shifts in community composition. During previous work (Chapter 4) we found that some dependent plants were entirely absent in areas that had been highly affected by

hurricanes, whereas others became more plentiful. Of those species that were present across most of the different impact sites, we detected a shift in abundance along the vertical axis. For example, the bromeliad *T. butzii* had its highest abundance between 40-50 m at very low impacted sites. On high impacted sites, the abundance peak shifted towards lower branches (20-40 m). The shift in abundance of *T. butzii* with increasing hurricane impact may be a reflection of the reduction of the species' fundamental niche. *T. butzii* is a somewhat unusual bromeliad, as it prefers more shaded conditions compared to most atmospheric species (Benzing et al. 1978). Thus, *T. butzii* was mostly observed on the abaxial branch surfaces (*pers. obs.* by the lead author). The increase in solar radiation and VPD as a result of wind damage (see Chapter 3 and 4) may have made the upper canopy less favorable for this species.

In contrast the abundance of many orchid species increased with hurricane impact in the upper canopy. The differences in response among species, was possibly a reflection of the different niche requirements and differing degrees of susceptibility to disturbance (e.g. to changes in the microclimate) among species. The tank bromeliads *Catopsis hahnii* and *C. floribunda*, for example, occurred frequently in the upper canopy in high impact sites. These species have been reported to be relatively well adapted to exposed conditions [i.e. presence of a tank, medium number of trichomed scales and rapid maturity (Benzing and Renfrow 1971, Hietz et al. 2002)]. Dependent plant species that are less well adapted to exposed condition are thus expected to diminish or shift in their distribution to more favorable microsites. In the case of the mesic *W. werckleana*, we found that this species occurred between 0-20 m across all levels of hurricane impact, but with a lower abundance on sites that were more impacted by hurricanes. In a previous chapter (Chapter 4) we showed that this species was also often associated with intermediate open canopies. As *W. werckleana* is limited to the lower canopy, possibly as a result of physiological limitation (Pittendrigh 1948, Reyes-García et al. 2008), any further negative shift in the canopy microclimate (e.g. as a result of more severe canopy damage) could result in the loss of this species from such sites. Losses would be concentrated among individuals that are small in size, as they are most susceptible to changes in the micro-environment (Zotz and Thomas 1999).

5.4.2. Dependent plant responses along the branch

Our results showed that holo-epiphytes had particular location preferences between the adaxial and abaxial surface of the branches. Epiphytes (i.e. holo- and hemi-epiphytes) had higher cover values on the adaxial surfaces. The adaxial surfaces in the canopy were possibly physiologically more suitable (Zotz and Vollrath 2002) due to optimal microclimate conditions. Also these sites often accumulate more soil and leaf litter (Sillett and Pelt 2007) and are more supportive for the development of large bryophyte mats (Sillett et al. 1995). However, as branches vary in their exposure to environmental condition, we would expect to see differences between branches across the canopy. For example, branches that experience higher irradiation and lower RH would become less suitable. This would include branches that are located on the outer canopy or braches that were exposed to extreme conditions as a result of sudden changes in the canopy structure (e.g. gap formation). The latter could be a result of wind damage (Lawton 1990).

Wind damage can increase canopy openness (Chapter 4), increase temperature and irradiation and decrease RH (Chapter 3). The adaxial surface of a branch would therefore be more vulnerable to these changes. Thus, epiphytes are likely to be less abundant on the adaxial surfaces in areas that have been impacted more as a result of wind damage. Additionally, these branches are more likely to be stripped of epiphytes due to their exposed position. Post-perturbation recovery and colonization would most likely be the key community composition drivers on these branches (Turner et al. 1998). Initial colonization may be hampered, however, as changes in microclimate (Chapter 3) and less favorable growing conditions on the branch surface (e.g. absence of organic material such as bryophytes) may slow colonization. Nadkarni (2000) demonstrated that, after experimental branch stripping of all organic material, epiphyte colonization occurred from the abaxial branch surface. She suggested that the higher abundance of bryophytes and the resulting higher water-retention capacity of the abaxial branch surfaces, due to shading effects of the branch itself, had made these sites more suitable for colonization. During ontogeny, epiphytes are expected to grow towards the adaxial surface of the branch, as plants are increasingly relieved from water

stress due to their larger size (Zotz and Vollrath 2002). Although we did not assess colonization, we found that mean bryophyte cover was significantly reduced on high impact sites (by approximately 30%) and that vascular epiphyte abundance on adaxial branch surfaces was generally lower at high impacted sites compared to abaxial surfaces. However, we found statistically significant differences only at a family but not a community level.

The presence/absence of non-vascular epiphytes accounted for variation in the observed vascular dependent plant species richness and abundance. Vascular species richness was positively correlated with increased bryophyte cover and negatively correlated with increasing lichen cover. As bryophytes (León-Vargas et al. 2006) and lichens have shown to respond to changes in RH and temperature (Cornelissen et al. 2007), it was predicted that their cover will change as a function of these. Our data showed that lichen cover was negatively correlated with RH and positively with temperature; whereas bryophyte cover was positively correlated with RH and negatively with temperature. Our model suggested that temperature was a reasonable indicator for lichen cover, whereas RH in combination with height in the canopy was a reasonable indicator for bryophyte cover. It is likely that other environmental factors such as exposure and increased solar radiation are also important (Wolf 1994, Aragón et al. 2010). Similar results were found by Karger et al. (2012), who investigated epiphytic bryophyte cover as a proxy for air humidity in tropical rainforests. They concluded that epiphytic bryophyte cover was weakly positively correlated with RH but more closely negatively correlated with temperature and changes in elevation (highlands: 1800-3500 m asl. versus lowlands: < 1800 m asl.). Frahm (2003) has shown that epiphytic lichens and bryophytes require different habitats, which are often associated with different desiccation periods. High lichen cover is characteristic of habitats with long desiccation periods. The response of non-vascular epiphytes along the forest profile is probably a result of microclimate stratification and different levels of exposure to wind, to solar radiation and biotic competition.

The effect the abundance of non-vascular epiphytes had on vascular dependent plant species could have been driven by several factors. Vascular dependent plant richness was directly affected by non-vascular epiphytes, as

the occurrence of non-vascular epiphytes either promoted or inhibited the establishment and survival of vascular dependent plants. Experimental studies that have investigated this are rare and most studies are largely observational. For example, Zotz and Vollrath (2003) reported that vascular epiphytes were significantly associated with patches on palm trees in Panama that harbored more bryophytes. Callaway et al. (2001) reported positive as well as negative effects on the establishment of *Tillandsia usneoides* (L.) L. associated with the occurrences of lichen species. Their results showed that different tree species hosted different non-vascular epiphyte communities, the composition of which in return influenced (positively and negatively) the abundance of *T. usneoides.* These effects could be because of the allelopathic inhibition by lichens of the germination and growth of bryophytes and vascular epiphytes (Frahm et al. 2000) and/or due to differences in the competitive ability of vascular and non-vascular species during early stages of establishment (Marín et al. 2008).

The effects that non-vascular epiphytes have on vascular dependent plants has shown to be dependent on the latter's life-stage (Winkler et al. 2007). For example, bryophytes can be of great importance to the establishment of vascular dependent plants during an early stage of ontogeny (Marín et al. 2008), particularly during times of drought. Bark that is covered in bryophytes has a higher water and nutrient retention capacity and also may facilitate physical attachment of vascular dependent plants during succession compared to bare bark (Nadkarni 2000). In our study, the importance of bryophytes on vascular dependent plants differed between different vascular life-forms. For example, we found that holo-epiphytes in particular were more frequently observed on branches with high bryophyte and low lichen cover, whereas many of the climbing species (nomadic vines and climbers) were more associated with branches that had a lower bryophyte and higher lichen cover. It needs to be noted that high bryophyte cover was also strongly associated with larger branches and high lichen cover with smaller branches. Therefore, it is not clear whether the vascular dependent plant response was a result of non-vascular epiphyte abundance, of an area-effect (e.g. larger branches) or of differences in the microclimate across the canopy. For example, larger branches are generally older (allowing greater time to be colonized) and are more frequently

located in the lower canopy where RH is higher (Chapter 3 and 4). Likewise, it is possible that changes in the microclimate caused a positive feedback, allowing non-vascular epiphytes (particularly bryophytes) to flourish on large branches and thereby promoting the establishment and survival of vascular species.

Vascular dependent plant richness and abundance were weakly correlated to different bark properties. Dependent plant richness increased with branches that had a rougher and more deeply fissured bark and decreased on branches that had a very flaky bark. Holo-epiphytes in particular were more frequently associated with deeply fissured and rough-textured bark. Generally, species from the Orchidaceae preferred branches that had a high bryophyte and low lichen cover, had a rough bark and were not flaky in texture. Most fern species were associated with branches that had a high surface area, a negative inclination (i.e. sloping downwards), a high bryophyte cover, a low lichen cover and a rough and non-flaky bark. Bromeliaceae species showed similar associations to ferns but showed little preference as to branch size. It has been reported that the texture of the bark can affect a dependent plant's ability to germinate (Vergara-Torres et al. 2010). Bark that is more deeply fissured and rougher is likely to accumulate more debris and particulates, compared to smooth or flaky bark, and is thus likely to be more suitable for establishment (ter Steege and Cornelissen 1989, de Andrade et al. 2009). The water-holding capacity of the bark has also been shown to affect the performance of epiphytes (Callaway et al. 2002); higher water-holding capacity is associated with thicker, rougher and more deeply fissured bark. On the contrary, flaky bark would make the facilitation more difficult (Zimmerman and Olmsted 1992).

In conclusion, different epiphytic life-forms, families and species responded differently across the multidimensional spectrum of climatic and structural habitat conditions in the canopy. We found that holo- and hemi-epiphytes in particular showed strong responses to different properties along the branch, whereas most other life-forms showed much weaker responses. The abundance of different dependent plant species was shown to have shifted vertically as a result of different levels of past hurricane impact. The shift of particular species within and between canopies appeared to be the result of

structural and microclimatic alterations of the canopy following hurricane damage. As demonstrated in Chapter 3 and 4, the microclimate and the dependent plant community response differed with increasing hurricane impact. Canopies that were more affected by hurricanes had a more open canopy, higher VPD and a lower diversity of dependent plants. This change in the canopy microenvironment with increasing hurricane impact thus had negative effects on both the non-vascular and vascular dependent plant abundance at a branch level. As forest canopies are self-maintaining organic structures that may quickly recover from perturbation events, it can be predicted that micro-environmental conditions may also recuperate swiftly. Certain mechanically dependent plant species will gain competitive advantage, eventually restoring dependent plant community structure across the canopy to a situation reflecting pre-hurricane impact patterns (Goode and Allen 2008). It is likely that the pre-hurricane dynamic equilibrium may be rather rapidly regained, as has been demonstrated in a number of other taxa (Waide 1991a, b, Wunderle et al. 1992).

Chapter 6

Epiphytes in Honduras: a biogeographical overview of the vascular epiphyte flora and its floristic affinities to other Central American regions

6.0. Abstract

Previous estimates of vascular epiphytes have revealed that approximately 9% of all global plants are epiphytes and that in some countries they contribute approximately one quarter of the total plant diversity. Early estimates of vascular epiphytes from the neotropics have mostly overestimated the total number of epiphytes at a given locality, due to systematic misconceptions and or the use of different life-form classification systems. Moreover, some Central American countries such as Honduras have so far been neglected in any epiphyte surveys. In this paper, we present for the first time epiphyte data from Honduras. The data were extracted from recent published checklists and compared to floristic inventories from other Central American localities including Costa Rica, Panama, Nicaragua and Belize. Our database included a total of 2797 flowering-plant epiphytes. We reported a total of 886 vascular epiphytes (Angiosperms and Pteridophytes) from 237 genera and 29 families from Honduras, representing 11% of the country´s total vascular flora. Orchidaceae had the highest contribution to the epiphyte flora (55%), followed by Polypodiaceae (13.7%), and Bromeliaceae (11.3%). Two distinctive biogeographic clusters were detected separating South-Central and North-Central localities. Honduras had the most floristic affinity to Nicaragua and Belize. In addition, a detailed floristic survey of Cusuco National Park, Honduras, a montane forest region, revealed that epiphytes in Honduras may contribute over 20% of the total vascular flora in a particular area. The results of this study highlight the importance of epiphytes in Honduras relative to other Central American localities. We believe that more targeted epiphyte collection efforts need to be undertaken in Honduras and adjacent areas, as the majority of detailed epiphyte surveys in the Central American region have focused on Panama and Costa Rica.

6.1. Introduction

Honduras is still one of the least botanically studied countries in Central America. Although the numbers of plant collections have been relatively high in the past, most collection efforts have been very localized (Gentry 1978). Early botanical surveys dating from the nineteenth century include collections by A. Sinclair, G. Barcley and R.B. Hinds of the H.M.S. *Sulphur* voyage (Bentham 1844) and by W.B. Hemsley who published *Biologia Centrali-Americana*, a catalogue of Central American plants (Hemsley 1879-1888). Later, there were localized collections by Samuel J. Record (Record 1927), Paul C. Standley (Standley 1930, 1931, 1934) and T.G. Yuncker (Yuncker 1938, 1940). During the 1950's – 1990's botanical contributions to the Honduran Flora were mostly limited, with a few publications describing smaller additions to the Flora. In 1996 Cyril Hardy Nelson Sutherland and colleagues published a catalogue of the Honduran Pteridophytes (Nelson et al. 1996), which was followed by the most substantial record of the Honduran Flora to date; the *Catálogo de las plantas vasculares de Honduras* (Nelson 2008). However, Honduras still lacks a published Flora. According to the two published catalogues, the Honduran Flora encompasses 651 species of Pteridophytes (Nelson et al. 1996) and 7950 species of Spermatophytes (Angiosperms and Gimnosperms) (Nelson 2008). These number need to be revised soon as new discoveries continue to be made (Ulloa et al. 2010, Batke and Hill 2013).

Epiphyte surveys in Honduras are particularly scarce and, to our knowledge, most epiphytes have only been included as part of general vegetation surveys, e.g. Standley (1931) on the flora of Lancetilla Valley near Tela; Molina (2002 *unpublished*) on Bromeliaceae in a cloud forest in Departamento el Paraiso; Duenas (2002 *unpublished*) a guide to 55 orchid species at the Biological Reserve Yuscaran; Piątek et al. (2012) on ferns and lycophytes in Celaque National Park. We are only aware of one study that specifically focused on epiphytes, in the Copan region in the SW of Honduras (Decker et al. 2011) [see Decker (2009 *unpublished*) for more detail]. In biogeographical comparisons of the Neotropical epiphyte flora, Honduras has so far been entirely neglected (Gentry 1982, Gentry and Dodson 1987b, Nieder et al. 1999, Cascante-Marín and Nivia-Ruíz 2013). In a recent overview of Neotropical epiphytes diversity,

Cascante-Marín and Nivia-Ruíz (2013) included, for Central America, only Panama, Costa Rica, Nicaragua and Belize, with no references to Honduras, El Salvador and Guatemala.

Current estimates of Neotropical epiphyte diversity indicate that approximately 10-17% of all vascular plants are epiphytes (Ibisch et al. 1996, Cascante-Marín and Nivia-Ruíz 2013). This is similar to global estimates of 9-10% (Kress 1986, Zotz 2013b). However, the proportion of epiphyte species varies considerably between different regions (Cascante-Marín and Nivia-Ruíz 2013). As pointed out by G. Zotz (Zotz 2013a, b), differences in epiphyte estimates may be partially attributed to differences in the ways in which life-forms are classified [see Zotz (2013b) for a more detailed discussion]. The classification of plants into the epiphytic life forms has never been straightforward and many attempts have been made to encompass the different life-history strategies of different species (Benzing 1987, 1990). Many life-form categories blend into one another as emphasised by Kelly (1985), with examples of the plasticity of individual species which makes their categorization difficult. Currently, the most useful life-form classification for mechanically dependent plants (Kelly 1985) divides species into six categories: holo-epiphytes, primary hemi-epiphytes, nomadic vines (includes secondary hemi-epiphytes), climbers (lianas and vines), stranglers and hemi-parasites (i.e. mistletoes) (Zotz 2013a, b). Only holo-epiphytes and primary hemi-epiphytes (including stranglers) are accepted by Zotz (2013b) as epiphytes. It is essential, in any study of epiphyte diversity, to be explicit about the classification used to facilitate comparisons (Moffett 2000, Zotz 2013a).

In the present study, we amended Cascante-Marín and Nivia-Ruíz (2013) work on the Neotropical vascular epiphytes of Central America, by including floristic information on Honduran epiphytes and by excluding species that do not fall within the definition of Zotz (2013b). The aims of the study were (1) to present data on the epiphytic diversity of the Cusuco National Park and an overview of the vascular epiphyte plants of Honduras and its contribution to the country's flora, (2) to evaluate the geographic affinities of the Honduran epiphyte flora in the context of the Central American region.

6.2. Methodology

6.2.1. Cusuco National Park

Cusuco National Park (CNP) is located in the Departments of Santa Barbara and Cortés in north-west Honduras (15°32'31"N, 88°15'49"W; Figure 6.1). Cusuco is situated within a mountainous, high-rainfall region, with a mean annual precipitation of approximately 2500 mm (Baker 1994). The wet season is between May and November. Maximum elevation is 2242 m asl. The forest in CNP consists of a complex mosaic of forest types, dominated by mixed broadleaved and pine forests in the core zone. *Liquidambar* (Hamamelidaceae), *Pinus* (Pinaceae) and *Quercus* (Fagaceae) are the principal tree genera (maximum forest height of emergent canopy was approximately 65 m). The families Melastomataceae, Lauraceae, Rubiaceae and Euphorbiaceae are also well represented. At the highest elevations a well-defined elfin forest is present. The buffer-zone has a minimum elevation of zero meters (data were only collected above 660 m) and consists of secondary vegetation (mostly pine), coffee plantations, small settlements and agricultural pastures.

6.2.2. Epiphyte database

We compiled a database of vascular epiphytes for CNP, Honduras, Costa Rica, Nicaragua, Panama and Belize. Data for CNP comprised floristic data from two surveys conducted by the lead author in 2012 and 2013, a floristic inventory provided by the Operation Wallacea Botany Team lead by D.L. Kelly (2004-2013; http://opwall.com/) and a floristic inventory from C. Nelson from 1993 (Baker 1994). The inventory by the lead author focused on canopy dependent plants, voucher specimens are deposited at the herbaria in Trinity College Dublin (TCD). Rope climbing methods were employed in ten 150 × 150-m plots across the park and the six largest trees were sampled for all mechanically dependent plants. The inventories by D.L. Kelly and C. Nelson focused on terrestrial life-forms, although opportunistic samples of the dependent flora were also made. The database for Honduras was compiled using published floristic information from the literature. We used Nelson (2008) and Nelson et al. (1996) as source-data.

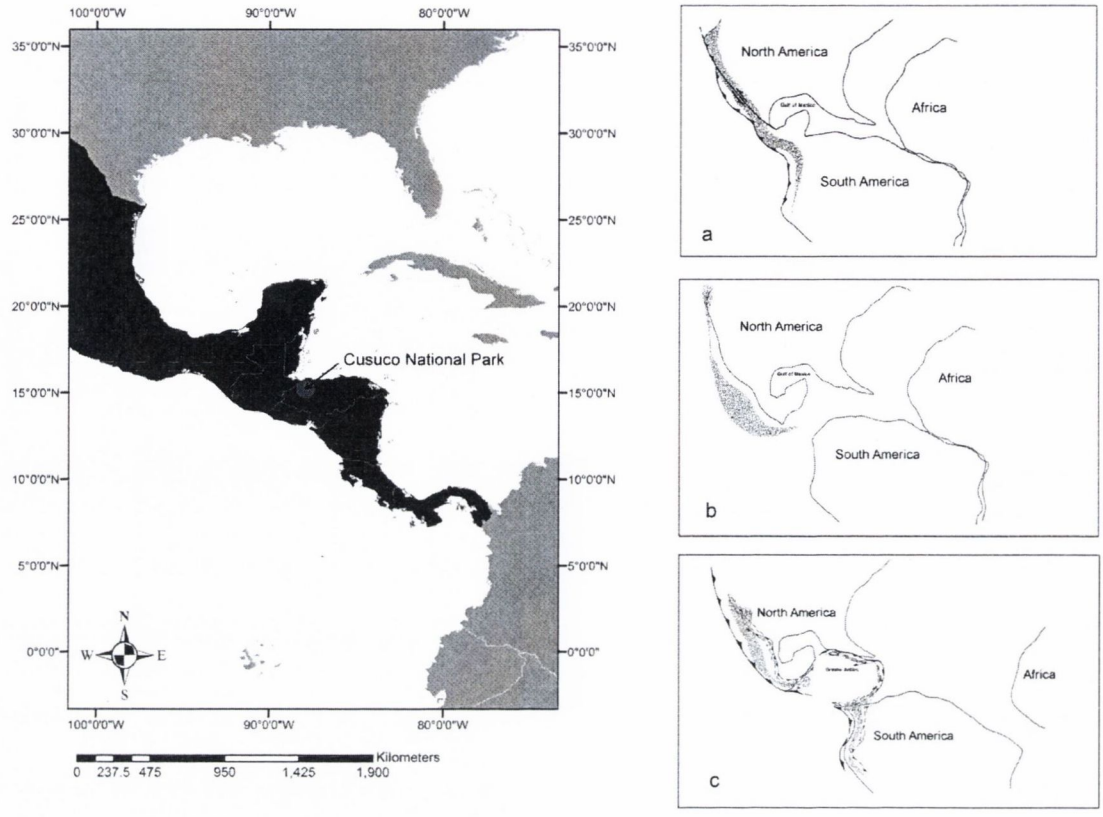


Figure 6.1 Maps of Central America including parts of South and North America. The figure on the left presents the current configuration of Central America and the location of Cusuco National Park in Honduras. The figures on the right present late Jurassic (A), early Cretaceous (B) and Eocene (C) plate configurations of North and South America. Barbed lines are subduction zones where one tectonic plate moves under another plate. Dashes show distribution of magmatic arcs. Figures A-C were adopted from Coney (1982) and Janzen (1983).

The recent overview by Zotz (2013b) was followed to identify all the families and genera that were known to include epiphytes. To identify the different life-forms, we cross-referenced individual species to the Flora de Nicaragua (Tomo I-IV) (Stevens et al. 2001, Gomez 2009), Flora of Guatemala (Standley and Steyermark 1946), Flora Mesoamericana (Davidse et al. 1995) and the TROPICOS Database of the Missouri Botanical Garden (http://www.tropicos.org). The floristic data for other Central American countries

including Costa Rica, Nicaragua, Panama and Belize were assembled by A. Cascante-Marín [data summarized in Cascante-Marín and Nivia-Ruíz (2013)].
In our database the botanical family and species name was documented for each region. Following Cascante-Marín and Nivia-Ruíz (2013) and Zotz (2013b), we included only records of holo-epiphytes, hemi-epiphytes, stranglers and facultative epiphytes. Accidental epiphytes and hemi-parasitic epiphytes from the families Eremolepidaceae, Loranthaceae and Viscaceae (Santalaceae) were not included. For taxonomic classification at the family level we followed Zotz (2013b) and Mabberley (2008). We followed Zotz's (2013b) recommendation and excluded secondary hemi-epiphytes (i.e. nomadic vines) (Moffett 2000, Zotz 2013a). Most of these species in our region belonged to genera from the Araceae such as *Anthurium*, *Monstera*, *Philodendron* and *Syngonium*. Moreover, we also excluded taxa that did not fully satisfy the definition of a primary hemi-epiphyte or holo-epiphyte (Zotz 2013b). These included several taxa from the families Gesneriaceae, Hydrangeaceae and Piperaceae and all taxa from the Marcgraviaceae. The exclusion of these taxa from the database resulted in a substantial reduction (n = 222) in the number of species for each region relative to those included by Cascante-Marín and Nivia-Ruíz (2013). We excluded a total of 177 species from Panama, 170 species from Costa Rica, 72 species from Nicaragua and 29 species from Belize. Records for Honduras that could not be assigned a life-form category were excluded from the database. This will have led to a more conservative estimate of the number of epiphytes in Honduras. Finally, to avoid taxonomic synonymy or redundancy in our data we used the TROPICOS Database and the third edition of Mabberley (2008).

6.2.3. Data analysis

To allow comparison to other studies, we used the same analytical methods as described by Cascante-Marín and Nivia-Ruíz (2013). The contribution of epiphytic plants between different countries was compared using an 'epiphyte quotient'. The epiphyte quotient expressed the contribution of epiphytes to the total flora and was expressed as a percentage. As the epiphyte quotient does not take into account the areal extent of the region under investigation, we

needed to express the relative richness of epiphytes with regards to the total area of each region. We used the model $S = cA^z$ to express the number of species (S) in relation to area (A). The letters c and z are constants that were defined as $z = 0.14$ and $c = S/A^z$. The relative richness (c) was rescaled using a scale from 0-1. A value of 1 was assigned to the locality that had the highest c-value and therefore the highest relative richness [see Cascante-Marín and Nivia-Ruíz (2013) for more detail].

The floristic similarity of epiphytes between localities was estimated using Jaccard's similarity coefficient, Sj (Krebs 1999). This method was used as it allowed comparisons of data sets with unequal numbers of absent species. Only angiosperms were used in the floristic comparison among localities, as we did not have adequate information on Pteridophytes from most Central American countries.

6.3. Results

6.3.1. Epiphyte richness at CNP and Honduras

The data base for CNP comprised 912 species of vascular plants (Table 6.1) and nearly 33% corresponded to epiphytic species. Of the 305 mechanically dependent species recorded, including hemi-parasites, the following three groups accounted for half the total (Appendix A2.1), 23% (n = 70) were from the family Orchidaceae, 19% (n = 58) were ferns from the group Polypodiaceae *s.l.* and 10.5% (n = 32) were from the family Bromeliaceae. Most of the dependent flora (62%) in CNP was represented by holo- and hemi-epiphytes. The epiphyte quotient for the CNP was 20.7%.

In our database for Honduras we identified a total of 886 species of epiphytes from 237 genera and 29 families. Most of the epiphytes (71.6%) were represented by only three families: Orchidaceae, Polypodiaceae and Bromeliaceae. Only 13 of the 29 families were represented by more than ten species of epiphytes (Table 6.2). The epiphyte quotient for Honduras was approximately 11% of the total flora (Table 6.2).

Table 6.1 Overall life-form composition of the vascular flora for Cusuco National Park, Honduras. The total number of families, genera and species for the different life-forms are presented.

Life-form	No. families	No. genera	No. species
Terrestrial	120	299	607
Holo-epiphyte	14	56	168
Primary hemi-epiphyte	8	10	21
Strangler	1	1	3
Nomadic vine	1	5	20
Climber	35	53	79
Hemi-parasite	2	7	14
Total	181	431	912

6.3.2. Geographic affinities of the Honduran epiphyte flora

The exclusion of 222 species from Cascante-Marín and Nivia-Ruíz (2013) database that did not fulfill Zotz's (2013b) definition of an epiphyte, produced a total of 585 Dicotyledonae (s.l.) and 2212 Monocotyledonae. The ten most diverse Central American epiphyte genera comprised 43.8% of all the species from our database and were mainly represented by orchid genera (Table 6.3). Costa Rica had the highest epiphyte quotient followed by Panama, Nicaragua, Honduras and Belize. CNP had a high epiphyte quotient, but this was in relation to a vegetation that was largely forest and specifically sampled for epiphytes (Table 6.4). Comparing the relative number of epiphytes species (following the relationship $S = cA^z$) between Central American countries indicated that Honduras had a similar relative number of epiphytes to Nicaragua. Costa Rica and Panama had the highest relative numbers of epiphytes and Belize the lowest (Table 6.4).

Table 6.2 (next page) Taxonomic overview of Honduras' epiphyte flora and comparison with Neotropical and global figures. Data for the Neotropics and the global estimates are summarized from the literature. H = Honduras; N = Neotropics; G = Global; 1 = Kress (1986); 2 = Gentry & Dodson (1987); 3 = Wiehler (1983); 4 = Zotz (2013); 5 = Cascante-Marín & Nivia-Ruíz (2013); *nd* = no data available; asterisk = Pteridophytes.

Family	No. genera with epiphytes[H]	No. epiphytic species[H]	Total no. species[H]	Epiphyte quotient (%)[H]	Epiphyte quotient (%)[N]	Epiphyte quotient (%)[G]
Orchidaceae	145	488	641	76	67[(2)]	69[(4)]
Bromeliaceae	13	100	125	80	46[(1)]	56[(4)]
Polypodiaceae*	17	44	76	58	93[(1)]	86[(4)]
Piperaceae	1	36	164	22	24[(2)]	25[(4)]
Hymenophyllaceae*	2	36	48	75	67[(1)]	55[(4)]
Aspleniaceae*	4	24	59	41	59[(1)]	55[(4)]
Dryopteridaceae*	4	21	38	55	15[(2)]	20[(4)]
Cactaceae	9	18	59	31	7[(2)]	8[(4)]
Gesneriaceae	5	15	57	26	20[(3)]	14[(4)]
Moraceae	1	13	67	19	37[(2)]	36[(4)]
Lycopodiaceae*	2	13	20	65	50[(1)]	49[(4)]
Araceae	2	12	95	13	42[(2)]	8[(4)]
Pteridaceae* (Vittariaceae)	8	11	14	79	100[(2)]	9[(4)]
Clusiaceae (Guttiferae)	1	8	31	26	9[(2)]	38[(4)]
Begoniaceae	1	7	32	22	nd	3[(4)]
Ericaceae	5	6	32	19	23[(2)]	15[(4)]
Nephrolepidaceae*	1	6	10	60	nd	67[(4)]
Melastomataceae	2	4	149	3	14[(2)]	6[(4)]
Solanaceae	2	4	173	2	nd	2[(4)]
Lomariopsidaceae*	1	4	4	100	nd	0.4[(4)]
Selaginellaceae*	1	3	33	9	nd	2[(4)]
Araliaceae	1	2	27	7	10[(2)]	4[(4)]
Rubiaceae	2	2	266	1	4[(2)]	1[(4)]
Blechnaceae*	1	2	18	11	nd	nd
Asteraceae (Compositae)	2	2	414	0	nd	0.2[(4)]
Psilotaceae*	1	2	2	100	nd	100[(4)]
Oleandraceae*	1	1	1	100	nd	50[(4)]
Crassulaceae	1	1	3	33	nd	2[(4)]
Asparagaceae	1	1	88	1	nd	0.5[(4)]
Total (all)	**237**	**886**	**7950**	**11.1**	**10[(2)]-17.5[(5)]**	**9.0[(4)]**
Total (Angiosperms)	**194**	**719**	**7298**	**9.0**	**10.9[(2)]**	**10.1[(4)]**
Total (Pteridophytes)	**43**	**167**	**652**	**2.1**	**1.1[(2)]**	**1.2[(4)]**

The diversity of epiphyte species deviated between different localities (x^2 test: $P < 0.01$). A strong cluster was observed between South-Central (i.e. Costa Rica and Panama) and North-Central American localities (Belize, Nicaragua and Honduras) (Figure 6.2). The greatest similarity was between Costa Rica and Panama (Sj-value = 98.7%). The epiphyte flora of Honduras was taxonomically most similar to that of neighboring Nicaragua, Sj-value = 89.8% (Figure 6.2, Figure A4.1).

Table 6.3 Composition of the Central American epiphytic flora (flowering plants) as represented by the ten most important, in terms of species number, epiphyte families and genera.

Family composition		Generic composition	
Family	**Total epiphytes**	**Genera**	**Total epiphytes**
Orchidaceae	1738	*Epidendrum* (Orchidaceae)	221
Bromeliaceae	266	*Pleurothallis* (Orchidaceae)	220
Araceae	160	*Anthurium* (Araceae)	145
Piperaceae	113	*Maxillaria* (Orchidaceae)	140
Ericaceae	81	*Lepanthes* (Orchidaceae)	123
Gesneriaceae	74	*Peperomia* (Piperaceae)	113
Melastomataceae	65	*Tillandsia* (Bromeliaceae)	73
Moraceae	42	*Stelis* (Orchidaceae)	72
Cyclanthaceae	41	*Werauhia* (Bromeliaceae)	64
Cactaceae	39	*Oncidium* (Orchidaceae)	55

Table 6.4 Species richness of vascular epiphytes (including Pteridophytes) from selected regions of Central America. Data from Nicaragua, Costa Rica, Panama and Belize were modified from Cascante-Marín and Nivia-Ruíz (2013). The relative number of species represents the number of epiphyte (i.e. holo-epiphytes, primary hemi-epiphytes, stranglers and facultative) species in relation to the area of the region ($S = cA^z$).

Region	Elevation asl. (m)	Area (km^2)	Epiphyte flora	Epiphyte quotient (%)	Relative number of species
Costa Rica	0-3820	51100	2,441	25.6	1
Panama	0-3475	78200	1,816	20.7	0.70
Nicaragua	0-2438	129794	985	18.7	0.35
Honduras	0-2870	112492	886	11.1	0.33
Belize	0-1124	22963	385	11.3	0.18
CNP	660-2242	234	189	20.7	0.16

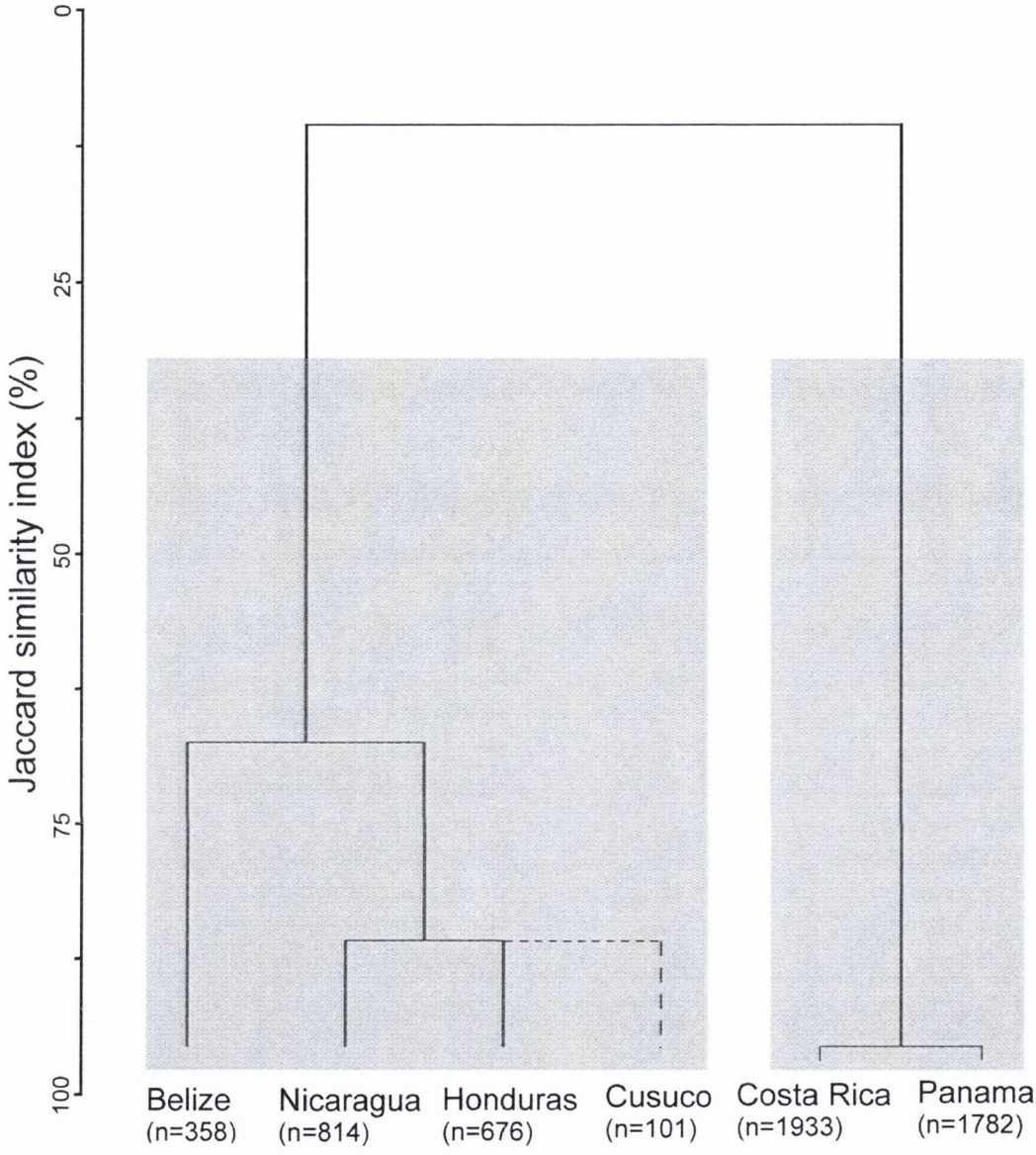


Figure 6.2 Comparison of floristic affinities among angiosperm epiphytic floras across Central America. The total number of species is given for each locality. A Jaccard similarity index was used as distance measure and flexible beta as a group linkage method for the clustering.

6.4. Discussion

The systematic contribution of vascular epiphytes (Angiosperms and Pteridophytes) to the global plant diversity was recently estimated to

approximately 9%, which represents a total of 27,614 species from 913 genera in 73 families (Zotz 2013b). Similar global estimates have been made elsewhere, with approximations of 10% (Madison 1977, Kress 1986, Gentry and Dodson 1987b). The latter figure appears to correspond to early Neotropical estimates (Gentry and Dodson 1987b, Ibisch et al. 1996) but has been demonstrated to vary significantly between different regions (Cascante-Marín and Nivia-Ruíz 2013). It is important to note that early estimates of Neotropical epiphytes often included other mechanically dependent plants such as secondary hemi-epiphytes. As previously pointed out by Moffett (2000) and more recently by Zotz (2013a), the term "secondary hemi-epiphyte" has often been misused in the literature and has resulted in much confusion in the categorization of species. Secondary hemi-epiphytes differ in their ecology to species that are truly epiphytic (Holbrook and Putz 1996, Zotz 2013a, b). Many estimates for epiphytes are thus likely to be exaggerated using the criteria of Zotz (2013b).

Our analysis, which excluded secondary hemi-epiphytes and other taxa that did not fully satisfy Zotz's criteria (e.g. Marcgraviaceae), differed from earlier Central American estimates between 0.8% and 1.8% (Cascante-Marín and Nivia-Ruíz 2013). The exclusion of species (total number of excluded species = 222) across the localities did not affect the overall observed epiphyte quotient patterns but somewhat changed the floristic affinities among localities. In Central America, the highest number of epiphytes was recorded from Costa Rica, followed by countries such as Panama, Nicaragua, Honduras and Belize. This is still in agreement with Cascante-Marín and Nivia-Ruíz (2013). However, floristically they found that Nicaragua was relatively close to Costa Rica and Panama in southern Central America, whereas our study found that Nicaragua was more similar to north Central American localities. Including Honduras into the analysis resulted in a split of Nicaragua from the South-Central American group. The exclusion of certain species (e.g. nomadic vines) resulted in an approximately 15% decreases in floristic similarity between the South-Central and North-Central American countries. The decrease in floristic similarity can be attributed to the high diversity and degree of endemism of certain species such as nomadic aroids (Araceae) in South-Central America (Grayum 1990,

Croat 1998). Our analysis excluded most species of the Araceae. We omitted a total of 127 nomadic species from Panama, 107 from Costa Rica, 47 from Nicaragua and 24 from Belize. Of the 150 species of Araceae reported from Panama, 55% are endemic to the region, whereas Honduras and Nicaragua have each only a single endemic species (Croat 1998). Moreover, many of the aroids from North-Central America were also found in South-Central America, which resulted in the lower observed similarity following their exclusion.

The floristic difference among Central American countries reflects the differing representation of biogeographical elements from North and South American floras. Past geological, climatic and biogeographical events are recognized to have played important roles in the current distribution of epiphytes in the Neotropics (Haffer 1969, Gentry 1982, 1988, Knapp and Mallet 2003, Morawetz and Raedig 2007, Graham 2011, Cascante-Marín and Nivia-Ruíz 2013). During the late Jurassic the Caribbean-Middle American region formed, as part of the supercontinent Pangaea (Figure 6.1A). South America was still attached to Africa at that point, which predetermined South America's position with respect to North America. By the early Cretaceous South America started separating from North-America (Figure 6.1B). In the late Cretaceous a chain of magmatic arcs formed, connecting Central America with Ecuador (Coney 1982). Thus, the connection between nuclear Central America and South America was reestablished by mostly interrupted island arcs in the late Cretaceous (Gentry 1982). The degree of connectivity and the number of islands that were above sea level however, are not known. In the late Neogene with the formation of the Central American trench and the associated uplifting of new volcanic islands (Figure 6.1C), the land bridge between South and Central America coalesced forming a land connection across the Isthmus of Panama (Graham 1973, 2011). Of particular importance to the migration of plant species was the uplift of the Andes during the Neogene, which resulted in a rapid increase in plants from the Gondwanan families in South America. With the closing of the Panamanian Isthmus, Laurasian taxa migrated southwards and Gondwanan families migrated northwards. This migration, particularly from the south, resulted in the strong Gondwanan elements observed in South-Central America. The flora of Panama and Costa Rica are therefore more influenced by

Godwanan families, whereas North-Central American countries such as Honduras have much stronger Laurasian and north temperate floristic elements (Graham 2011). This was also reflected in our results, as our cluster analysis identified one distinctive South-Central and another North-Central American group.

The strong South-North floristic dissimilarity of epiphytes was also reflected in individual taxonomic groups. For example, within the Ericaceae the genera *Anthopteropsis*, *Didonica* and *Utleya* were characteristic of the South-Central American group. These genera have mostly been associated with low-elevation and permanent cloud forests in Panama and Costa Rica (Luteyn 2002). Similar, the North-Central American group was characterized by the genus *Satyria*. Kron and Luteyn (2005) pointed out that *Satyria* has undergone more recent speciation in North-Central America than most Ericaceae following the introduction via dispersal from the northern Andes (Kron and Luteyn 2005). Similarly, we found evidence that the number of epiphytic species from the genus *Columnea* (Gesneriaceae) decreased from the South-Central (mainly Costa Rica) to the North-Central American group (60% difference in the number of species between Costa Rica and Belize). DNA chloroplast analysis of *Columnea* has suggested that the radiation of this genus has most likely occurred in Central America and that the epiphytic habit arose more than once (Smith and Sytsma 1994b). Bird dispersal has been attributed to be one of the most likely contributing factor to explain the distribution of *Columnea* in some Central America regions (Smith and Sytsma 1994a). This was also reported for other families, where biotic and long-distant dispersal are believed to be more important than past plate-tectonic activities (Renner et al. 2001, Pennington and Dick 2004, Christenhusz and Chase 2013). Other geographical features such as the Talamancan montane range in Costa Rica and Panama could also have been important in the radiation of some species (Kohlmann et al. 2010, Perret et al. 2013).

In our database for Honduras we recognized a total of 886 epiphytes species from 237 different genera and 29 different families. As expected, epiphytism was mostly restricted to a small number of taxonomic groups including

Orchidaceae (n = 488), Pteridophytes (n = 167) and Bromeliaceae (n = 100). The dominance of these groups from Honduras is consistent with other studies (Gentry and Dodson 1987b, Kreft et al. 2004, Küper et al. 2004, Cascante-Marín and Nivia-Ruíz 2013, Zotz 2013b). Orchids in particular are the most dominant family in Neotropical inventories. Of the 2797 angiosperm epiphyte species reported here from Central America, orchids' alone contributed to over 60% of the total vascular epiphyte flora. The high numbers of epiphytic orchids in many tropical inventories reflect their high genetic and morphological variation, their short life-cycle and the higher niche differentiation in tropical forest canopies compared to forest floors (Benzing 1990, Ackerman and Ward 1999, Gravendeel et al. 2004). Globally almost 25,000 orchid species have been described, of which approximately 18,000 are epiphytic (Gravendeel et al. 2004). Members of Polypodiaceae, a Pteridophyte family, were the second largest epiphytic group from Honduras. Pteridophytes, in general, accounted for approximately 2.2% of all vascular epiphytic plants in Honduras, which was slightly above Neotropical (1.1%) and global (1.2%) estimates for that group (Gentry and Dodson 1987b, Zotz 2013b).

Honduras had an epiphyte quotient of approximately 11%, which was similar to Belize, but only half that of Panama (approximately 21%) and less than half that of Costa Rica (approximately 26%). Compared to Nicaragua, Honduras had a similar relative number of epiphytes for its land-surface area, whereas the relative numbers of epiphytes for Costa Rica and Panama were much higher. Although, Honduras is almost twice the size of Panama and Costa Rica, it had a much lower number of epiphyte species. As epiphytes mostly occur in humid forest habitats, the variation in the relative number of species observed could be a result of differences in forest cover among countries. According to the FAO (2010), Honduras had a forest cover of approximately 50,000 km^2 (46%) in 2010, whereas forest cover in Nicaragua (26%) and Panama (44%) was lower. Belize had the highest forest cover (61%), followed by Costa Rica (51%). Botanical efforts in documenting the flora of Central American countries may also account for the observed differences in epiphyte diversity; the botanical exploration and documentation of Costa Rica and Panama´s flora have received more attention during the last decades.

Moreover, it is important to note that the epiphyte quotient in a particular locality depends on the number of non-epiphytic taxa sampled. For example, CNP had an epiphyte quotient of approximately 20% and a relatively low number of species for its size. The high epiphyte quotient is likely the result of a survey bias towards terrestrial woodland species and the relative number of species was consequently based on an area that was mainly forest.

Our data suggest a decreasing geographic trend in vascular epiphyte diversity in Central America, from Panama to Belize. It is possible that some of the floristic difference, which was observed between the South-Central and North-Central American regions, is attributed to limited specialized collection efforts particularly in North-Central American countries. Our database did not include all Central American floras and it is likely that the total number of epiphytes in North-Central America would be higher if Guatemala and El Salvador were included. Guatemala in particular has a very rich flora (Standley and Steyermark 1946) and it is believed that Guatemala's flora is the most species-rich flora for angiosperms in Central America (Morawetz and Raedig 2007). As most epiphytes have a very small distribution range (Küper et al. 2004), including epiphyte inventories from Guatemala and El Salvador would most certainly increase the total number of epiphytes found in North-Central America. Belize, El Salvador and Honduras have currently no complete published floras and even the checklists for vascular plants in El Salvador (Calderón and Standley 1941) and Guatemala [with the exception of orchids (Cameron 2000)] require substantial revisions.

Most research on the mechanically-dependent flora in Central America has been conducted in South-Central American countries such as Panama and Costa Rica (Nadkarni and Matelson 1992, Patino et al. 1999, Laube and Zotz 2006, Marín et al. 2008, Zotz and Schultz 2008, Cascante-Marín et al. 2009, Caceres et al. 2011, Caceres et al. 2013), with less focus on North-Central American regions such as Nicaragua (Atwood 1984), Belize (Catling 1997), El Salvador (Méndez et al. 2010), Guatemala (Catling and Lefkovitch 1989, Nesheim and Økland 2007) and Honduras (Decker et al. 2011). The only country in parts of Mesoamerica that has been covered relatively well in

epiphyte studies is Mexico (Hietz and Hietz-Seifert 1995, Wolf and Konings 2001, Hietz et al. 2002, Wolf 2005, Wolf and Flamenco-S. 2006, Scheffknecht et al. 2010, Vergara-Torres et al. 2010). Collections in Honduras have mostly been sporadic and have generally focused on the terrestrial flora. Thus many species, particularly widely distributed species, are still absent from collections. Botanical collections have often focused on the southern and north-western coast, with little contribution from mountainous regions (Gentry 1978). It has been shown that sites that are located in mountain cloud forest are often more epiphyte rich (Cardelus et al. 2006), highlighting the need to have more targeted collections efforts in such areas.

It is likely that the number of epiphytes in Honduras, and other 'epi-floristically' neglected countries such as El Salvador, Guatemala and Belize, will rise with more targeted sampling efforts. For example, our survey in CNP discovered previously unknown epiphytes from the Park, Honduras and/or Mesoamerica [e.g. Batke and Hill (2013)]. This is important given current anthropogenic pressures to many forests in Honduras and elsewhere in Central America (Southworth and Tucker 2001, Bonta 2005). We therefore propose that future epiphyte sampling efforts in Honduras focus more on moist montane forests, as these locations have been less impacted by forest degradation and are more likely to reveal further additions to the Honduran epiphyte flora.

Chapter 7

7.0. General discussion

In this thesis, I set out to provide baseline information on the vascular dependent flora of Cusuco National Park, Honduras (CNP) and to make floristic comparisons between the epiphytic floras of CNP, Honduras and other Central American countries. I also aimed to investigate the response of mechanically dependent plants (Kelly 1985) to past hurricane impacts and different environmental and structural variables across forest trees in CNP. To achieve the former I aimed to develop a basic hurricane model that would allow me to predict past hurricane impacts in CNP. Furthermore, I aimed to use the model to compare the microclimate and dependent plant responses across trees that had been affected differently by past hurricanes (Figure 7.1).

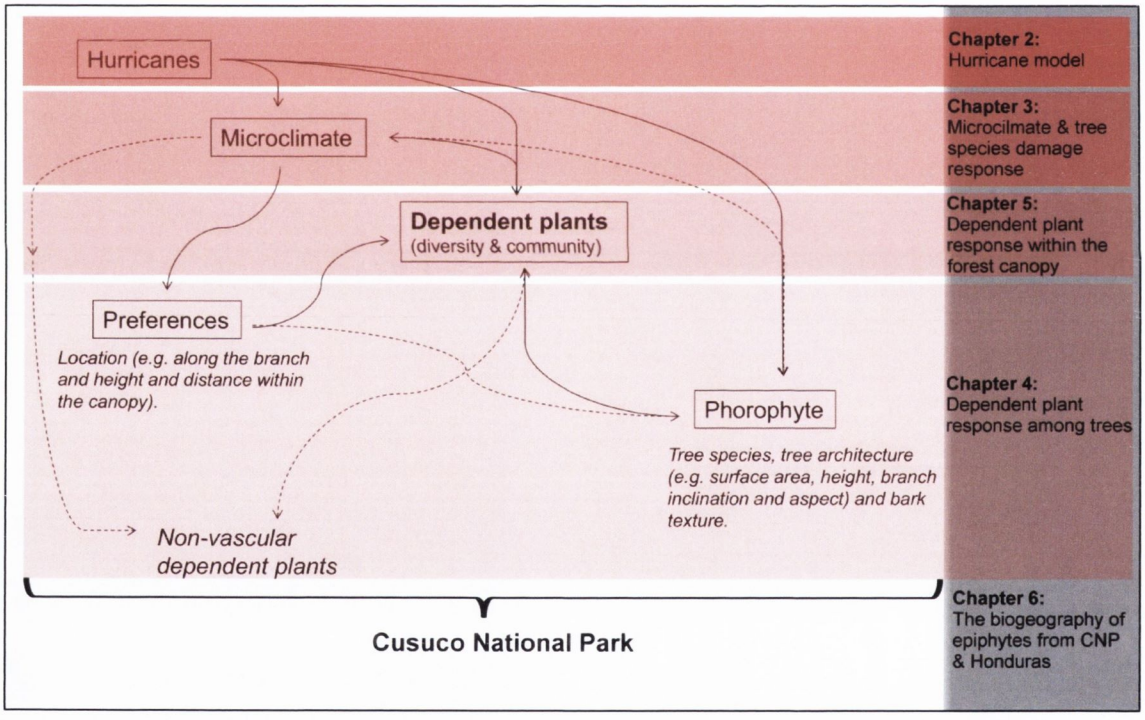


Figure 7.1 Thesis overview. The flow chart illustrates how the different chapters are linked. Solid arrows represent direct thesis objectives and dashed arrows indirect objectives.

It has widely been established that disturbance events such as storms, wild fires, landslides, seismic activities, disease outbreaks and anthropogenic

activities can be strong drivers in the dynamics of forest ecosystems (Everham and Brokaw 1996, Ayres and Lombardero 2000, Dale et al. 2001, Wells et al. 2001). In 2000, global forest cover was approximately 33 million km^2 (Hansen et al. 2010), of which 2.3 million km^2 were lost between 2000 and 2012 as a result of disturbance (Hansen et al. 2013). The highest losses were observed in tropical regions (increase in loss = 2101 km^2 yr^{-1}). In Central America, forest loss has been approximately 10-20% since 2000 (Hansen et al. 2013) and was often the result of the expansion of agricultural landscapes (Kammerbauer and Ardon 1999, Wright 2005). The impacts of disturbances on forests are often very localized and are dependent on the size, duration and severity of the event (Turner and Dale 1998). Large, infrequent disturbances are usually much rarer and it is still unclear whether they qualitatively differ from small/frequent events, due to the lack of available long-term data.

Hurricanes, in particular, have been shown to cause significant alterations to forest systems (Basnet et al. 1992, Ensor 2009). Damage from hurricanes includes uprooting of trees, branch damage, defoliation of the canopy, gap formation and indirect alteration of the forest microclimate (Boose et al. 1994, Everham and Brokaw 1996). Most studies that have assessed the impact of hurricane damage on forest canopies have focused on damage following the impact of one individual event [e.g. Goode and Allen (2008)]. As the long-term recovery of a forest can be very slow (Lugo et al. 2000), it is important to incorporate the cumulative effects of disturbances over a given time period. In Chapter 2 I developed a model that allowed the prediction of the past impact of hurricanes in CNP. The model allowed me to identify areas that had been differentially impacted by hurricanes over a 15-y period and was computed from the frequency of hurricanes, the maximum wind velocity of individual hurricanes and the topographic exposure of the study site. Using tree assessment methods, I validated the model on the ground and showed that the model explained approximately 70% of physical branch damage observed on trees (Chapter 2). However, branch damage varied between different tree species (Chapter 3). For example, conifer trees (*Pinus* spp.) had more branch damage than angiosperms (mainly *Liquidambar styraciflua* and *Quercus* spp.). This was possibly the result of differences in canopy architecture and wood strength

between tree types (e.g. density and elasticity) (Xi et al. 2008). Angiosperms had a more closed canopy compared to conifers; canopy openness increased in high elevation sites where trees had been more impacted by past hurricane storms (Chapter 4). Although hurricane impact has been relatively low in CNP over the last 15 years (Chapter 2), structural alteration of the forest canopy could still be detected long after the passing of such events (the last severe hurricane that impacted CNP was hurricane Mitch in 1998). My results have also highlighted the need to incorporate tree identity in forest assessments, as the scale of disturbance often reflects the species (Xi et al. 2008) and stands (Brokaw and Walker 1991, McCallum et al. 2007) vulnerability to storm damage.

Any structural change in the forest canopy as a result of hurricanes is likely to have a knock-on effect on the microenvironment within the canopy (Turton and Siegenthaler 2004). As demonstrated in Chapter 3, tree canopies that were more impacted by hurricanes had a higher vapour pressure deficit (VPD) compared to canopies that were less impacted (12% of changes in VPD was explained by relation to hurricane incidence). The increase in VPD consequent on hurricane impact was the result of a decrease in relative air humidity (RH) and an increase in temperature. The consequences of changes in VPD through the canopy with increasing disturbance level will vary spatially and with the scale of the disturbance. For example, the upper canopy is likely to vary more in its degree of change compared to the lower canopy (Brokaw and Walker 1991, Turton and Siegenthaler 2004, Turton 2013). This was also observed in Chapter 3, however, with less difference between the upper and middle canopy layer. Changes in the canopy microenvironment might result in the thermophilization (a shift in species as a result of changes in climate) of lower-layer plant communities (de Frenne et al. 2013). Mechanically dependent plants in particular have been shown to respond to anthropogenically induced microclimate alterations (Rapp and Silman 2014). Thus, it can be predicted that similar alterations caused by hurricanes will also have important impacts on dependent plant communities (Goode and Allen 2008, Mújica et al. 2013) and will vary spatially among different disturbance sites.

The damage a hurricane can cause to the dependent flora can be summarized in direct and indirect effects. Direct effects refer to physical damage such as blow down or damage to the tissues, whereas indirect effects refer to damage to the host tree. To identify whether it is possibly to detect indirect differences in the community structure of mechanically dependent plants following hurricane disturbance (i.e. changes as a result of structural and microclimate alterations of the canopy), I compared trees that had been exposed to different levels of past hurricane damage (Chapter 2, 4 and 5). I showed that the dependent plant diversity decreased significantly on trees that had been affected more by hurricanes and that the community composition differed among sites with different levels of hurricane impact (Chapter 4). Within individual trees, mechanically dependent life-forms varied in their response to hurricane damage (Chapter 5). Holo- and hemi-epiphytes responded much more strongly than climbers, nomadic vines and mistletoes. The response was manifested in a shift of their distribution (e.g. decrease/increase in abundance) along the vertical forest profile (Chapter 5) and was most likely the result of structural and microclimatic alterations in the canopy (e.g. increased canopy openness and increases in VPD – Chapter 3 and 4). It has previously been reported that mechanically dependent plants vary in their response to alterations of the canopy (Larrea and Werner 2010), most likely as a result of different eco-physiological requirements (Saldaña et al. 2005, Gianoli et al. 2012). As an example, I found that species that were adapted to stressful environments (e.g. desiccation tolerant species) were more frequently observed on highly impacted sites (Chapter 4). Currently now research has investigated the community response of mechanically dependent plants after hurricane damage and also no research has so far identified the community responses after repetitive perturbation. My work was therefore a first attempt to quantify plant community responses between host trees that had been differently affected by past hurricanes.

The dependent plant community response along a gradient of past hurricane impact was clearly evident when comparing very high and very low impact sites. However, intermediate impact sites were less distinct (Chapter 4). As pointed out in Chapter 4, this may reflect the recovery response of the forest, as

highly impacted sites take longer to recover. The recovery of dependent plants following disturbance can sometimes be very slow (Nadkarni 2000) and may depend on the species under investigation (Patino et al. 1999). Communities that are less affected are more likely to recover faster, whereas recovery will be much slower in areas that have been more disturbed, due to the slow growth rate, the high juvenile mortality and the late maturation of many dependent plants (Zotz 1995, Schmidt and Zotz 2002, Laube and Zotz 2003, Werner and Gradstein 2008). Other structural and environmental factors (e.g. the presence/absence of non-vascular epiphytes and the bark texture of the tree) are also important in driving the dependent plant community composition among and within trees (Chapter 4 and 5).

The presence of non-vascular dependent plants, i.e. epiphytic bryophytes and lichens, was shown to have strong effects on the vascular dependent flora (Chapter 5). The presence of bryophytes is likely to have facilitated the abundance and species richness of vascular dependent plants, whereas a high cover of lichens was related to low vascular species richness. However, the responses differed among dependent life-forms. Life-forms that were more dependent on the structural support of a branch, such as holo- and hemi-epiphytes, had a higher species abundance on branches with high bryophyte cover and a larger surface area. Climbers, nomadic vines and hemi-parasitic mistletoes on the other hand were more abundant on smaller branches that had higher cover of lichens (Chapter 5). It is possible that the high cover of bryophytes facilitated vascular holo- and hemi-epiphyte abundance as a result of the bryophytes' ability to retain higher levels of water and nutrients (Nadkarni 2000). It has been shown that bryophytes are particularly important at an early establishment stage, as branches that are covered in bryophyte mats provide more optimal growing conditions compared to bare bark (Winkler et al. 2007, Marín et al. 2008). The responses of different life-forms to different host (Chapter 4) and branch characteristics (Chapter 5) reflect each life-form's ecological requirements throughout the course of its life-cycle. For example, nomadic vines and climbers are connected to the forest floor during the early stages of their ontogeny, which makes them less dependent on the structural

qualities of the branch (e.g. bryophyte cover). In contrast, holo- and hemi-epiphytes are more constrained by a canopy-dependent life style.

Mechanically dependent plants in CNP differed in their responses to environmental and structural conditions at a plot, tree and branch level. I showed that the response to these conditions varied with scale (plot, tree and branch) and between different dependent life-forms, families and species (Chapters 4 and 5). On a landscape level, geographical and climatic factors such as elevation, exposure and VPD were more important (44.4% of the community similarity - Chapter 4), whereas at a local level, structural features of the host tree were more important (30% of the community similarity between trees – Chapter 4; see also Chapter 5). The effects of hurricanes on the dependent plant flora consequently varied at different scales. On a landscape level, hurricanes are likely to decrease the number of dependent plants considerably (Loope et al. 1994) (Chapter 4); the recovery is likely to be slow and will depend on the plants' ability to survive, recover or re-establish (Benavides et al. 2006). If the damage to the area is low, recovery is likely to be swift. If the damage is high and disturbances are more frequent, it is likely that recovery will be slow (Rodriguez-Robles et al. 1990). If an area has been damaged severely as a result of hurricane occurrence (the extreme being complete loss of all mechanical support), the recovery rate of dependent plants will be dependent on the recovery response of the forest and the availability of viable propagules for colonization (Wolf 2005, Mondragon et al. 2006).

At an individual tree and branch level, the effects of hurricane damage will depend on the tree's geographical location and its proneness to damage (Chapter 3). Trees that are more likely to lose limbs or to be uprooted will show higher levels of dependent plant damage and slower levels of recovery. Trees that are located in areas that have been more affected by hurricanes are thus more likely to have an open canopy (as a result of structural damage to the canopy) and they will experience higher levels of irradiation, higher temperatures and lower RH (Chapter 3 and 4). Dependent plants will therefore suffer more, physiologically. This can result in the absence of certain species from such canopies, causing a change in the dependent community to more

tolerant species (Chapter 4) or a shift of species along the vertical profile to more suitable locations (Chapter 5). In CNP, the overall damage caused by hurricanes has been relatively low and the occurrence of hurricanes has been infrequent over the last 15-yrs (Chapter 2; also see Chapter 3 for a comparison of the likelihood of hurricane occurrence in the Caribbean). Nevertheless, I was still able to detect apparently hurricane-related differences between sites that had been exposed to different levels of hurricane damage and I was able to demonstrate that the changes in microclimate and the responses of mechanically dependent plants can be detected long after the occurrence of such events.

The long-term effects of hurricanes on the dependent plant community in CNP are difficult to predict. It is likely that current climate trends may increase the frequency and/or intensity of hurricane-related impacts in the Caribbean (Mann and Emanuel 2006, Jury et al. 2012, IPCC 2014). If the frequency of such events stays relatively low, it seems unlikely that changes in the overall dependent community will be perceptible. However, if the frequency of hurricane events increases, recovery will be delayed, which could result in the loss of many dependent plants from some areas at least. For example, Cascante-Marín and Nivia-Ruíz (2013) have argued that the low diversity of epiphytes (holo- and hemi-epiphytes) in Cuba might be the result of frequent hurricane damage. As Cuba is an island, proximity to the nearest seed source could limit the establishment capacity of many dependent plants.

Cusuco is relatively rich in its dependent flora, with a total of 305 reported mechanically dependent species (Chapter 6). Epiphytes in particular contributed to over 20% of the total vascular flora in CNP, which is significantly higher compared to the epiphyte quotient of Honduras (11.1%; Chapter 6). Moreover, recent survey efforts revealed new botanical records to the Park, Honduras and/or Mesoamerica. For example, during my collections in 2012 and 2013, I identified 13 species (+ 10 unconfirmed) of vascular plants that were new records to the Honduran Flora (Table 7.1); including one species that was a new record for Mesoamerica (Appendix 3). As CNP is less geographically and biologically isolated, compared to islands such as Cuba, the risk of hurricane

related losses to the Park is likely to be less important. It is more probable that other threats such as deforestation, agricultural encroachment and climate change are of greater concern to dependent plants in CNP (Nadkarni and Solano 2002, Gradstein 2008, Hsu et al. 2011).

Table 7.1 Plants that were collected by the author in Cusuco National Park and were new records to the Honduran flora. Only 13 of the 23 species have been fully identified and verified as new records. Life-forms: NV = nomadic vine; C = climber; H = holo-epiphyte; Ph = primary hemi-epiphyte; Tree = terrestrial tree; P = hemi-parasite.

Family	Species	Life-form	Distribution (after TROPICOS.org)
Araceae	*Anthurium* cf. *montanum* Hemsl.	NV	Guatemala, Mexico
Araceae	*Philodendron* cf. *grayumii* Croat	NV	Costa Rica, Panama
Araceae	*Philodendron* cf. *ligulatum* var. *ovatum* Croat	NV	Panama
Araceae	*Philodendron inequilaterum* Liebm.	NV	Brazil, Ecuador, Mexico
Araceae	*Philodendron lentii* Croat & Grayum	NV	Costa Rica, Ecuador, Nicaragua, Panama
Araceae	*Rhodospatha latifolia* Poepp.	NV	Bolivia, Brazil, Ecuador, French Guiana, Peru, Venezuela
Begoniaceae	*Begonia* cf. *confusa* L.B. Sm. & B.G. Schub.	C	Guatemala
Bromeliaceae	*Tillandsia montana* Reitz	H	Brazil
Dryopteridaceae	*Elaphoglossum ambiguum* (Mett. ex Christ) Alston	H	Bolivia, Columbia, Ecuador, Panama, Peru, Venezuela
Gesneriaceae	*Columnea guatemalensis* Sprague	Ph	Guatemala, Mexico
Loranthaceae	*Psittacanthus* aff. *minor* Kuijt	P	Nicaragua
Orchidaceae	*Lepanthes* cf. *inaequalis* Schltr.	H	Belize, El Salvador, Guatemala
Orchidaceae	*Lepanthes vilchezii* F.L.Archila	H	Guatemala
Orchidaceae	*Maxillaria* aff. *biolleyi* (Schltr.) L.O. Williams	H	Costa Rica, Panama
Orchidaceae	*Maxillaria histrionica* (Rchb. f.) L.O. Williams	H	Columbia, Mexico, Venezuela
Orchidaceae	*Prosthechea vitellina* (Lindl.) W.E. Higgins	H	Mexico
Orchidaceae	*Stelis* cf. *hirsuta* (Garay) Garay	H	Ecuador
Piperaceae	*Piper* aff. *ottoniifolium* C. DC.	C	Columbia, Costa Rica, Ecuador, Panama
Polypodiaceae	*Polypodium puberulum* Schltdl. & Cham.	H	Costa Rica, El Salvador, Mexico
Polypodiaceae	*Serpocaulon lasiopus* (Klotzsch) A.R. Sm.	H	Bolivia, Caribbean, Columbia, Ecuador, Peru, Venezuela
Rosaceae	*Prunus rhamnoides* Koehne	Tree	Belize, Costa Rica, Guatemala, Mexico, Panama
Schlegeliaceae	*Schlegelia* cf. *spruceana* Bureau & K. Schum.	C	Brazil, Guyana, Venezuela
Vitaceae	*Cissus trifoliata* (L.) L.	C	Caribbean, Ecuador, Guatemala, Mexico, Nicaragua, USA, Venezuela

7.1. Limitations and recommendations

I identified three key limitations to this research. The hurricane model that was developed in Chapter 2 was simplistic in some regards. To calculate the impact of hurricanes in CNP I assumed that all hurricanes were circular in section. Moreover, I did not include changes in precipitation and in wind dynamics that might have occurred as a result of different vegetation types and local wind turbulences. Hurricanes are very dynamic weather fronts that change in size and shape throughout their life-time (Boose et al. 2001). Most hurricane models

do not incorporate sudden changes in size, due to the complexity of these systems; it has been argued that basic radial models are often sufficient for model computations (Vickery et al. 2000). Another simplification was the exclusion of precipitation events from the model. Heavy precipitation that is often associated with hurricane winds can be a major cause of tree uprooting due to soil erosion (Philpott et al. 2008). For example, there is evidence from CNP that major landslides occurred during hurricane Mitch in 1998, which caused extensive tree uprooting in some parts of the Park (pers. com. D.L. Kelly 2012). The database from the National Oceanic and Atmospheric Administration (NOAA) that was used to compute the hurricane model (Chapter 2) did not include any information on precipitation for individual hurricanes. It was therefore not possible to include precipitation as a factor in the final model.

Additionally, it has been pointed out that wind dynamics on a local scale can change as a result of different vegetation types and local turbulences (Peltola 1996). The physiognomy of the forest in CNP has only been assessed in a small number of plots at a few locations within the park; our overview of the park as a whole is still very limited. To overcome issues of geographical coverage, it is possible to use high resolution imagery or laser rangefinders from light airplanes or helicopters to determine the physiognomy of forest stands (Asner et al. 2002). The use of satellite remote sensing would also be more accurate and would simplify the need for intensive ground-damage validations (Wang et al. 2010). Due to resource limitations and limited satellite cover in the research area, these methods were not available to me. Moreover, the high cloud occurrence at CNP would have made the use of satellite images for a given time period difficult. Although different spatial resolutions and viewing angles can be used to overcome the issues of cloud interference, these methods are often costly and very time consuming (Strand et al. 2007). Having a higher and more detailed spatial resolution is desirable, but I believe that the relatively simplistic model used in this thesis was sufficient to achieve the project objectives. Future work that aims to identify hurricane-related impacts on mechanically dependent plants should incorporate local turbulences in its models, as these are likely to influence the damage and recovery dynamics of dependent plants within individual trees.

A further limitation of this study was the evaluation of the hurricane model on the ground. To evaluate the model, I correlated the model results to exposure and tree damage data that were collected within ten sample plots across CNP. The model performed well and I was able to explain approximately 70% of the recorded damage. However, due to the small number of sites and the low replication at a plot level, the geographical coverage was low. It is possible that, with further sampling effort, the model performance would have increased. I tried to incorporate descriptive accounts of hurricane related damage from surveys undertaken by the Operation Wallacea Forest Botany Team between 2004 and 2013 (Kelly et al. *unpubl. data*). However, it was not possible to satisfactorily include their results in my analysis. Ideally, the model evaluation would have included more sample plots across the park or incorporated damage assessments employing remote sensing technologies. Due to the high sampling intensity within each plot, a larger geographical coverage was not possible.

Lastly, I would like to point out some aspects of the dependent plant survey design that requires amendment. In this thesis I collected data on all mechanically dependent plants including holo- hemi-epiphytes, nomadic vines, climbers, stranglers and mistletoes. I sampled a total of 60 large trees [six in each plot (Zotz and Bader 2011)] and surveyed all dependent plants across the entire surface of each tree. My survey design was clearly insufficient to account for all life-forms equally. Climbers, hemi-epiphytes and nomadic vines in particular are much larger in size compared to holo-epiphytes. In most cases they are only represented by one or a few individuals per tree. This was reflected in the species accumulation curves for the different life-forms (Chapter 4). The number of climbers did not level-off under my sampling effort, suggesting that many additional species would have been added with additional sampling. According to the Chao and Jackknife estimates, I only found approximately half (n = 214) of the estimated number of dependent plants in CNP (Chapter 4) and it was mostly climbers and nomadic vines that were underrepresented in the database (Chapter 4 and 6). I recommend that further botanical surveys in CNP are undertaken on a larger geographical scale, using

a sampling design that accounts more equally for all the different life-forms (Gerwing et al. 2006, Wolf et al. 2009).

7.2. Future research

In this thesis I have shown that community responses of dependent plants can be detected long after the passing of hurricanes and that some species are likely to shift in their distribution within the canopy as a result of disturbances by past hurricanes. Most of the work presented in this thesis was based on data from observational research. Future work that evaluates the effect hurricanes have on mechanically dependent plants should incorporate more experimental examinations. For example, it is still unclear how much wind-force is required to dislodge and/or damage a dependent plant (*pers. com.* Zotz, G.). Larger individuals that have a weak rooting system and are located in the upper part of the canopy are more likely to be damaged by hurricane winds. Wind tunnel experiments could be used to identify the forces required to dislodge an individual. Comparisons could be made between different life-forms and species with different traits (e.g. rooting systems, sizes and shapes).

Trees that are located near the edge of a stand are more likely to be affected by storms (Foster 1988), which may increase the detachment of dependent plants (Oberbauer et al. 1996). Thus, the sheltering effect of other trees and of branches within individual trees have yet to be resolved. It is possible that epiphytes that grow in the inner canopy (e.g. in the fork), are less likely to be damaged. In addition, the substrate quality (e.g. bark texture and water retention capacity) may also be important. Few studies have assessed the long term recovery dynamics of dependent plants following hurricane damage (Robertson and Platt 2001), especially in relation to the recovery dynamics of the forest and the canopy microclimate. Long-term monitoring sites in hurricane-prone areas would provide valuable insight into the long-term recovery of dependent plants following hurricane perturbations.

Future work should also focus on the deficiency of dependent plant research in Honduras. In Chapter 6, I highlighted the need for further epiphyte research in

Honduras. Here I would like to extend this proposition by including other life-forms such as climbers, mistletoes and nomadic vines. Much of the lack of dependent plant research in Honduras can be attributed to a shortage of canopy access equipment and trained botanical experts. It would be desirable to invest resources into research projects that specifically address mechanically dependent plants and into the training of local staff to facilitate such research.

7.3. Concluding remarks

Mechanically dependent plants contribute over 11% of global vascular plant diversity (Benzing 1990, Nickrent et al. 1998, Gallagher and Leishman 2012, Zotz 2013b) and their floristic and ecological importance has frequently been recognized (Benzing 1987, 1990). Their structural dependency constrains them to their host tree. Sudden alterations in the host's environment will consequently affect the dependent plant community. Disturbance from large infrequent weather events such as hurricanes have been shown to cause great destruction to the dependent plant community (Goode and Allen 2008). The degree to which dependent life-forms respond to disturbance is dependent on the severity, duration and frequency of the disturbance event.

This research provided for the first time an account of the dependent plant flora in CNP and an overview of the epiphyte flora of Honduras. Moreover, this study was one of the first studies that assessed dependent plants in Honduras and their response to past hurricane impacts. It was shown that dependent plants showed correlations to hurricane related incidences by changes in their diversity, composition and distribution along individual host trees. It was also shown that other host characteristics such as the cover of non-vascular epiphytes are also important in explaining the distribution of different life-forms across the forest canopy. The data presented in this work has also highlighted the unique contribution of CNP's flora, to the floristic diversity of epiphytes in Central America. Cusuco is an important biodiversity hotspot for epiphytes and other mechanically dependent plants, which makes the Park of high importance to conservation. For example, many of the collected species were new records to the Honduran Flora and are currently only known from CNP.

It is recommended that future research should identify direct dependent plant response to hurricane wind damage and that hurricane models that predict hurricane related incidence in an area should include precipitation changes and local wind turbulences. Finally, as only limited information on mechanically dependent plants is available from CNP, it is recommended that more botanical and ecological research should be conducted within the Park.

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Appendices

Appendix 1.

Table A1.1 Epiphyte inventory from Cusuco National Park arranged by family. The life-forms refer to the epiphyte growth. Ph = primary hemi-epiphyte; H = holo-epiphyte; NV = nomadic vine; C = climber; S = strangler; P = parasite (mistletoe); A = accidental.

Family	Species	Life-form
Acanthaceae		
	Thunbergia aff. *alata* Bojer ex Sims	C
Apocynaceae		
	cf. *Mesechites* sp. 3	C
	Prestonia cf. *portobellensis* (Beurl.) Woodson	C
	Tintinnabularia murallensis J.K. Williams	C
	Climber 10	C
	Climber 11	C
Araceae		
	Anthurium cf. *montanum* Hemsl.	NV
	Anthurium scandens (Aubl.) Engl.	NV
	Anthurium sp. 1	NV
	Anthurium sp. 2	NV
	Monstera adansonii Schott	NV
	Monstera siltepecana Matuda	NV
	Philodendron aff. *sagittifolium* Liebm.	NV
	Philodendron cf. *advena* Schott	NV
	Philodendron cf. *grayumii* Croat	NV
	Philodendron cf. *ligulatum var. ovatum* Croat	NV
	Philodendron cf. *purulhense* Croat	NV
	Philodendron cf. *tenue* K. Koch & Augustin	NV
	Philodendron hederaceum (Jacq.) Schott	NV
	Philodendron inaequilaterum Liebm.	NV
	Philodendron inequilaterum Liebm.	NV
	Philodendron lentii Croat & Grayum	NV
	Philodendron sp. 1	NV
	Rhodospatha latifolia Poepp.	NV
	Syngonium podophyllum var. podophyllum Schott	NV
Araliaceae		
	Dendropanax arboreus (L.) Decne. & Planch.	A
	Dendropanax hondurensis M.J. Cannon & Cannon	A
	Oreopanax steyermarkii A.C. Sm.	Ph
	Climber 1	C
Aristolochiaceae		
	Aristolochia sp. 1	C
Asclepiadaceae		
	Climber 2	C
Aspleniaceae		
	Asplenium radicans L.	H
	Asplenium serra Langsd. & Fisch.	H
Asteraceae		
	Mikania aromatica Oerst.	C
	Mikania cf. *tonduzii* B.L. Rob.	C
	Sinclairia discolor Hook. & Arn.	Ph

Table A1.1 *Cont.*

Family	Species	Life-form
Begoniaceae		
	Begonia cf. *confusa* L.B. Sm. & B.G. Schub.	C
Bignoniaceae		
	Bignonia sp. 1	C
Blechnaceae		
	Blechnum ensiforme (Liebm.) C. Chr.	H
	Blechnum sp. 1	H
Bromeliaceae		
	Catopsis berteroniana (Schult. & Schult. f.) Mez	H
	Catopsis floribunda L.B. Sm.	H
	Catopsis hahnii Baker	H
	Catopsis montana L.B. Sm.	H
	Catopsis nitida (Hook.) Griseb.	H
	Catopsis nutans (Sw.) Griseb.	H
	Guzmania sp. 1	H
	Tillandsia butzii Mez	H
	Tillandsia guatemalensis L.B. Sm.	H
	Tillandsia juncea (Ruiz & Pav.) Poir.	H
	Tillandsia lampropoda L.B. Sm.	H
	Tillandsia magnusiana Wittm.	H
	Tillandsia makoyana Baker	H
	Tillandsia monadelpha (E. Morren) Baker	H
	Tillandsia montana Reitz	H
	Tillandsia multicaulis Steud.	H
	Tillandsia pruinosa Sw.	H
	Tillandsia punctulata Schltdl. & Cham.	H
	Tillandsia schiedeana Steud.	H
	Tillandsia seleriana Mez	H
	Tillandsia standleyi L.B. Sm.	H
	Tillandsia tricolor Schltdl. Cham.	H
	Tillandsia vicentina Standl.	H
	Tillandsia yunckeri L.B. Sm.	H
	Werauhia werckleana (Mez) J.R. Grant	H
Leguminosae (?)		
	Climber 3	C
Cactaceae		
	Epiphyllum crenatum (Lindl.) G. Don	H
	Epiphyllum thomasianum (K. Schum.) Britton & Rose	H
	Epiphyllum sp. 1	H
Clusiaceae		
	Clusia cf. *flava* Jacq.	Ph
	Clusia chanekiana Lundell	Ph
	Clusia minor L.	Ph
	Clusia salvini Donn. Sm.	Ph
Cunoniaceae		
	Weinmannia pinnata L.	A

Table A1.1 *Cont.*

Family	Species	Life-form
Cyclanthaceae		
	Dicranopygium gracile (Liebm. Ex Matuda) Harling	C
Lomariopsidaceae		
	Nephrolepis cordifolia (L.) C. Presl	H
	Nephrolepis pectinata (Willd.) Schott	H
Dioscoreaceae		
	Dioscorea convolvulacea Schltdl. & Cham.	C
Dryopteridaceae		
	Bolbitis bernoullii (Kuhn ex Christ) Ching	H
	Elaphoglossum ambiguum (Mett. ex Christ) Alston	H
	Elaphoglossum clewellianum Mickel	H
	Elaphoglossum guatemalense (Klotzsch) T. Moore	H
	Elaphoglossum lonchophyllum (Fée) T. Moore	H
	Elaphoglossum muscosum (Sw.) T. Moore	H
	Elaphoglossum petiolatum (Sw.) Urb.	H
	Elaphoglossum sp. 1	H
Ericaceae		
	Macleania insignis M. Martens & Galeotti	Ph
	Satyria warszewiczii Klotzsch	Ph
	Sphyrospermum cordifolium Benth.	Ph
	Vaccinium poasanum Donn. Sm.	Ph
	Climber 4	C
Gesneriaceae		
	Columnea guatemalensis Sprague	Ph
	Columnea sulfurea Donn. Sm.	Ph
	Drymonia oinochrophylla (Donn. Sm.) D.N. Gibson	C
	Drymonia sp. 1	C
Loranthaceae		
	Oryctanthus cordifolius (C. Presl) Urb.	P
	Psittacanthus aff. *minor* Kuijt	P
	Struthanthus orbicularis (Kunth) Blume	P
Lycopodiaceae		
	Huperzia linifolia var. linifolia (L.) Trevis	H
	Huperzia taxifolia (Sw.) Trevis.	H
Malpighiaceae		
	cf. *Tetrapterys* sp. 1	C
Marantaceae		
	Maranta sp. 1	C
Melastomataceae		
	Conostegia sp. 1	C
	Climber 5	C
	Climber 9	C
Menispermaceae		
	Cissampelos tropaeolifolia DC.	C

Table A1.1 *Cont.*

Family	Species	Life-form
Orchidaceae		
	Arpophyllum giganteum Hartw. ex Lindl.	H
	Arpophyllum medium Rchb. f.	H
	Bothriochilus macrostachyus (Lindl.) L.O. Williams	H
	Dichaea glauca Sw. (Lindl.)	H
	Dichaea muricatoides Hamer & Garay	H
	Dichaea neglecta Schltr.	H
	Dinema polybulbon (Sw.) Lindl.	H
	Elleanthus capitatus (Poepp. & Endl.) Rchb. f.	H
	Elleanthus cynarocephalus (Rchb. F.) Rchb. F.	H
	Elleanthus graminifolius (Barb. Rodr.) Løjtnant	H
	Elleanthus linifolius C. Presl.	H
	Encyclia sp. 1	H
	Encyclia tuerckheimii Schltr.	H
	Epidendrum mixtum Schltr.	H
	Epidendrum pseudoramosum Schltr.	H
	Epidendrum ramosum Jacq.	H
	Homalopetalum pumilio (Rchb.f.) Schltr.	H
	Isochilus major Schltdl. & Cham.	H
	Jacquiniella teretifolia (Sw.) Britton & P. Wilson	H
	Lepanthes cf. *inaequalis* Schltr.	H
	Lepanthes johnsonii Ames	H
	Lepanthes sp. 1	H
	Lepanthes vilchezii F.L.Archila	H
	Lycaste deppei (Lodd.) Lindl.	H
	Maxillaria aff. *biolleyi* (Schltr.) L.O. Williams	H
	Maxillaria cucullata Lindl.	H
	Maxillaria histrionica (Rchb. f.) L.O. Williams	H
	Maxillaria neglecta (Schltr.) L.O. Williams	H
	Nidema boothii (Lindl.) Schltr.	H
	Oncidium cf. *graminifolium* (Lindl.) Lindl.	H
	Oncidium sp. 1	H
	Pleurothallis cardiothallis Rchb. F.	H
	Pleurothallis dolichopus Schltr.	H
	Pleurothallis matudana C. Schweinf.	H
	*Pleurothallis s*p. 1	H
	Pleurothallis tuerckheimii Schltr.	H
	Prosthechea ochracea (Lindl.) W.E. Higgins	H
	Prosthechea pygmaea (Hook.) W.E. Higgins	H
	Prosthechea rhynchophora (A. Rich. & Galeotti) W.E. Higgins	H
	Prosthechea vitellina (Lindl.) W.E. Higgins	H
	Rhynchostele cordata (Lindl.) Soto Arenas & Salazar	H
	Scaphyglottis confusa (Schltr.) Ames & Correll	H
	Scaphyglottis fasciculata Hook.	H
	Stelis aprica Lindl.	H
	Stelis cf. *hirsuta* (Garay) Garay	H

Table A1.1 *Cont.*

Family	Species	Life-form
Orchidaceae (cont.)	*Stelis* cf. *parvula* Lindl.	H
	Stelis guatemalensis Schltr.	H
	Stelis immersa (Linden & Rchb. F.) Pridgeon & M.W. Chase	H
	Stelis sp. 1	H
	Stelis sp. 2	H
	Stelis villosa (Knowles & Westc.) Pridgeon & M.W. Chase	H
	Trichosalpinx sp. 1	H
Passifloraceae		
	Passiflora hahnii (E. Fourn.) Mast.	C
	Passiflora membranacea Benth.	C
Piperaceae		
	Peperomia deppeana Schltdl. & Cham.	Ph
	Peperomia glabella (Sw.) A. Dietr.	Ph
	Peperomia sp. 1	Ph
	Peperomia sp. 2	Ph
	Peperomia tenella (Sw.) A. Dietr.	Ph
	Piper aff. *ottoniifolium* C. DC.	C
Polygalaceae		
	Securidaca cf. *diversifolia* (L.) S.F. Blake	C
Polypodiaceae		
	Campyloneurum angustifolium (Sw.) Fée	H
	Cochlidium rostratum (Hook.) Maxon ex C. Chr.	H
	Lellingeria delitescens (Maxon) A.R. Sm. & R.C. Moran	H
	Melpomene anfractuosa (Kunz ex Klotzsch) A.R. Sm. & R.C.	H
	Melpomene xiphopteroides (Liebm. A.R. Sm. & R.C. Moran)	H
	Niphidium crassifolium (L.) Lellinger	H
	Pecluma alfredii (Rosenst.) M.G. Price	H
	Phlebodium pseudoaureum (Cav.) Lellinger	H
	Pleopeltis angusta Humb. & Bonpl. ex Willd.	H
	Pleopeltis astrolepis (Liebm.) E. Fourn.	H
	Pleopeltis crassinervata (Fée) T. Moore	H
	Pleopeltis macrocarpa var. macrocarpa (Bory ex Willd.) Kaulf.	H
	Pleopeltis mexicana (Fee) Mickel & Beitel	H
	Polypodium echinolepis Fee	H
	Polypodium furfuraceum Schltdl. & Cham.	H
	Polypodium hartwegianum Hook.	H
	Polypodium plebeium Schltdl. & Cham.	H
	Polypodium plesiosorum Kunze	H
	Polypodium polypodioides var. aciculare Weath.	H
	Polypodium polypodioides var. polypodioides (L.) Watt	H
	Polypodium puberulum Schltdl. & Cham.	H
	Polypodium sp. 1	H
	cf. *Polypodium* sp. 2	H
	Serpocaulon aff. *dissimile*	H
	Serpocaulon lasiopus (Klotzsch) A.R. Sm.	H
	Serpocaulon triseriale (Sw.) A.R. Sm.	H

Table A1.1 *Cont.*

Family	Species	Life-form
Pteridaceae		
	Vittaria graminifolia Kaulf.	H
	Vittaria sp. 1	H
Rosaceae		
	Rubus alpinus Macfad.	C
Rubiaceae		
	Galium hypocarpium (L.) Endl. ex Griseb.	C
Santalaceae		
	Antidaphne hondurensis Kuijt	P
	Phoradendron nitens Kuijt	P
Sapindaceae		
	Serjania rhachiptera Radlk.	C
Schlegeliaceae		
	Schlegelia cf. *spruceana* Bureau & K. Schum.	C
Selaginellaceae		
	Selaginella schizobasis Baker	H
Smilacaceae		
	Smilax domingensis Willd.	C
	Smilax subpubescens A. DC.	C
Solanaceae		
	Lycianthes chiapensis (Brandegee) Standl.	C
unknown		
	Climber 6	C
	Climber 7	C
	Climber 8	C
	Hemi-epiphyte sp. 1	Ph
Vitaceae		
	Cissus aff. *sicyoides* L.	C
	Cissus sp. 1	C
	Cissus trifoliata (L.) L.	C
	Vitis tiliifolia Humb. & Bonpl. ex Schult.	C
	Vitis Sp. 1	C

Appendix 2.

Table A2.1 Epiphyte inventory from Cusuco National Park, Honduras arranged by family. Combined list from surveys of S.P. Batke, D.L. Kelly (unpublished) and S.C. Nelson (Baker 1994). The life-forms are as follows: Ph = primary hemi-epiphyte; H = holo-epiphyte; NV = nomadic vine; C = climber; S = strangler; P = hemi-parasite.

Family	Species	Life-form
Acanthaceae		
	Thunbergia aff. *alata* Bojer ex Sims	C
Apocynaceae		
	Fernaldia pandurata (A. DC.) Woods var. *glabra*	C
	Prestonia cf. *portobellensis* (Beurl.) Woodson	C
	Tintinnabularia murallensis J.K. Williams	C
	cf. *Mesechites s* p. 3 (S.B.)	C
	Climber 10 (S.B.)	C
	Climber 11 (S.B.)	C
Araceae		
	Anthurium bakeri Hook. F	H
	Anthurium cf. *montanum* Hemsl.	NV
	Anthurium huixtlense Matuda	H
	Anthurium microspadix Schott	H
	Anthurium ochranthum C. Koch	NV
	Anthurium scandens (Aubl.) Engl.	NV
	Anthurium s p. 1 (S.B.)	NV
	Anthurium s p. 2 (S.B.)	NV
	Monstera adansonii Schott	NV
	Monstera siltepecana Matuda	NV
	Monstera sp. 1 (D.K.)	C
	Philodendron aff. *sagittifolium* Liebm.	NV
	Philodendron aurantifolium Schott	C
	Philodendron cf. *advena* Schott	NV
	Philodendron cf. *grayumii* Croat	NV
	Philodendron cf. *ligulatum* var. *ovatum* Croat	NV
	Philodendron cf. *purulhense* Croat	NV
	Philodendron cf. *tenue* K. Koch & Augustin	NV
	Philodendron glanduliferum Matuda	C
	Philodendron hederaceum (Jacq.) Schott	NV
	Philodendron inaequilaterum Liebm.	NV
	Philodendron inequilaterum Liebm.	NV
	Philodendron lentii Croat & Grayum	NV
	Philodendron s p. 1 (S.B.)	NV
	Rhodospatha latifolia Poepp.	NV
	Syngonium macrophyllum Engl.	C
	Syngonium podophyllum var. *podophyllum* Schott	NV
Araliaceae		
	Oreopanax capitatus (Jacq.) Decne. & Planch.	Ph
	Oreopanax steyermarkii A.C. Sm.	C
	Climber 1 (S.B.)	C
Aristolochiaceae		
	Aristolochia s p. 1 (S.B.)	C
Asclepiadaceae		
	Matelea or *Gonolobus* sp. 1 (D.K.)	C
	Climber 2 (S.B.)	C

Table A2.1 ***Cont.***

Family	Species	Life-form
Aspleniaceae		
	Asplenium auriculatum Sw.	H
	Asplenium cuspidatum Lam.	H
	Asplenium radicans L.	H
	Asplenium serra Langsd. & Fisch.	H
Asteraceae		
	Mikania aromatica Oerst.	C
	Mikania cf. *tonduzii* B.L. Rob.	C
	Sinclairia discolor Hook. & Arn.	Ph
Begoniaceae		
	Begonia cf. *confusa* L.B. Sm. & B.G. Schub.	C
Bignoniaceae		
	Bignonia s p. 1 (S.B.)	C
Blechnaceae		
	Blechnum ensiforme (Liebm.) C. Chr.	H
	Blechnum s p. 1 (S.B.)	H
Bromeliaceae		
	Aechmea luddemanniana A. L. (K. Koch) Brogn. Ex. Mez	H
	Catopsis apicroides (Schlecht. & Cham.) Baker	H
	Catopsis berteroniana (Schult. & Schult. f.) Mez	H
	Catopsis floribunda L.B. Sm.	H
	Catopsis hahnii Baker	H
	Catopsis montana L.B. Sm.	H
	Catopsis nitida (Hook.) Griseb.	H
	Catopsis nutans (Sw.) Griseb.	H
	Guzmania s p. 1 (S.B.)	H
	Tillandsia butzii Mez	H
	Tillandsia excelsa Griseb.	H
	Tillandsia guatemalensis L.B. Sm.	H
	Tillandsia juncea (Ruiz & Pav.) Poir.	H
	Tillandsia lampropoda L.B. Sm.	H
	Tillandsia leiboldiana Schlecht.	H
	Tillandsia magnusiana Wittm.	H
	Tillandsia makoyana Baker	H
	Tillandsia monadelpha (E. Morren) Baker	H
	Tillandsia montana Reitz	H
	Tillandsia multicaulis Steud.	H
	Tillandsia orogenes Standl. & L.O. Williams	H
	Tillandsia pruinosa Sw.	H
	Tillandsia punctulata Schltdl. & Cham.	H
	Tillandsia schiedeana Steud.	H
	Tillandsia seleriana Mez	H
	Tillandsia standleyi L.B. Sm.	H
	Tillandsia tricolor Schltdl. Cham.	H
	Tillandsia vicentina Standl.	H
	Tillandsia yunckeri L.B. Sm.	H

Table A2.1 ***Cont.***

Family	Species	Life-form
Bromeliaceae (*cont.*)	*Vriesea didistichoides* Mez	H
	Vriesea montana (L. B. Sm.) L. B. Sm. & Pittendr.	H
	Werauhia werckleana (Mez) J.R. Grant	H
Leguminosae(?)		
	Climber 3 (S.B.)	C
Cactaceae		
	Epiphyllum crenatum (Lindl.) G. Don	H
	Epiphyllum thomasianum (K. Schum.) Britton & Rose	H
	Epiphyllum s p. 1 (S.B.)	H
Clusiaceae		
	Clusia chanekiana Lundell	Ph
	Clusia flava Jacq.	Ph
	Clusia massoniana Lund.	Ph
	Clusia minor L.	Ph
	Clusia salvinii Donn. Sm.	Ph
	Clusia sp. 3 (D.K.)	Ph
Cucurbitaceae		
	Melothria pendula L.	C
	Psiguria triphylla (Mig.) C. Jeffrey	C
Cyclanthaceae		
	Dicranopygium gracile (Liebm. Ex Matuda) Harling	C
	Dicranopygium gracile ssp. *hondurense* Harl.	C
Dennstaedtiaceae		
	Hypolepis nigrescens Hook	H
Dioscoreaceae		
	Dioscorea convolvulacea Schldl. & Cham.	C
	Dioscorea cf. *composita* Hemsl.	C
Dryopteridaceae		
	Bolbitis bernoullii (Kuhn ex Christ) Ching	H
	Elaphoglossum ambiguum (Mett. ex Christ) Alston	H
	Elaphoglossum clewellianum Mickel	H
	Elaphoglossum guatemalense (Klotzsch) T. Moore	H
	Elaphoglossum latifolium (Sw.) J. Sm.	H
	Elaphoglossum lonchophyllum (Fée) T. Moore	H
	Elaphoglossum muscosum (Sw.) T. Moore	H
	Elaphoglossum paleaceum (Hook. & Grev.) Sledge	H
	Elaphoglossum petiolatum (Sw.) Urb.	H
	Elaphoglossum s p. 1 (S.B.)	H
	Lastreopsis effusa (Sw.) Tindale	H
Ericaceae		
	Macleania insignis Mart. & Gal.	Ph
	Satyria warszewiczii Klotzsch.	Ph
	Sphyrospermum cordifolium Benth.	Ph
	Vaccinium poasanum Donn. Sm.	Ph
	Climber 4 (S.B.)	C

Table A2.1 *Cont.*

Family	Species	Life-form
Fabaceae		
	Canavalia villosa Benth.	C
	Clitoria mexicana Link.	C
	Mucuna argyrophylla Standl.	C
Gesneriaceae		
	Ramirezella strobilophora (Rob.) Rose	C
	Columnea guatemalensis Sprague	Ph
	Columnea sulfurea Donn. Sm.	Ph
	Drymonia guatemalensis (C. V. Morton) D. N. Gibson	C
	Drymonia oinochrophylla (Donn. Sm.) D.N. Gibson	C
	Drymonia s p. 1 (S.B.)	C
Hymenophyllaceae		
	Trichomanes radicans Sw.	H
Lomariopsidaceae		
	Nephrolepis cordifolia (L.) C. Presl	H
	Nephrolepis pectinata (Willd.) Schott	H
Loranthaceae		
	Oryctanthus cordifolius (C. Presl) Urb.	P
	Psittacanthus aff. *minor* Kuijt	P
	Psittacanthus cf. *calyculatus* (DC.) G. Don.	P
	Struthanthus orbicularis (Kunth) Blume	P
Lycopodiaceae		
	Huperzia linifolia var. *linifolia* (L.) Trevis	H
	Huperzia taxifolia (Sw.) Trevis.	H
	Lycopodiella cernua (L.) Pichi-Sermolli	H
	Lycopodium clavatum L.	H
Malpighiaceae		
	Tetrapterys schiedeana Schltdl. & Cham.	C
	Stigmaphyllon lindenianum Adr. Juss. or *retusum* Griseb.	C
Marantaceae		
	Maranta s p. 1 (S.B.)	C
Marcgraviaceae		
	Marcgravia sp. 1 (D.K.)	C
Melastomataceae		
	Conostegia s p. 1 (S.B.)	C
	Topobea aeruginosa (Standl.) L. Wms.	C
	Climber 5 (S.B.)	C
	Climber 9 (S.B.)	C
Menispermaceae		
	Cissampelos tropaeolifolia DC.	C
Moraceae		
	Ficus insipida Willd.	S
	Ficus trigonata L. sensu lato	S
	Ficus sp. 1 (D.K.)	S
Orchidaceae		
	Arpophyllum giganteum Hartw. ex Lindl.	H

Table A2.1 *Cont.*

Family	Species	Life-form
Orchidaceae (*cont* .)	*Arpophyllum medium* Rchb. f.	H
	Arpophyllum spicatum La Llave & Lex.	H
	Bothriochilus macrostachyus (Lindl.) L.O. Williams	H
	Chondrorhyncha lendleyana Reichb. f.	H
	Dichaea glauca Sw. (Lindl.)	H
	Dichaea muricatoides Hamer & Garay	H
	Dichaea neglecta Schltr.	H
	Dichaea squarrosa Lindl.	H
	Dinema polybulbon (Sw.) Lindl.	H
	Elleanthus capitatus (R. Br.) Reichb. f.	H
	Elleanthus cynarocephalus (Rchb. F.) Rchb. F.	H
	Elleanthus graminifolius (Barb. Rodr.) Løjtnant	H
	Elleanthus linifolius C. Presl.	H
	Encyclia tuerckheimii Schltr.	H
	Encyclia s p. 1 (S.B.)	H
	Epidendrum mixtum Schltr.	H
	Epidendrum paniculatum Ruiz & Pavón	H
	Epidendrum pseudoramosum Schltr.	H
	Epidendrum radicans Pavón ex Lindl.	H
	Epidendrum ramosum Jacq.	H
	Epidendrum verrucosum Sw.	H
	Homalopetalum pumilio (Rchb.f.) Schltr.	H
	Isochilus major Schltdl. & Cham.	H
	Isochilus sp.1 (D.K.)	H
	Jacquiniella cobanensis (Ames & Schulta) Dressler	H
	Jacquiniella teretifolia (Sw.) Britton & P. Wilson	H
	Lepanthes cf. *inaequalis* Schltr.	H
	Lepanthes disticha Rich. & Gal.	H
	Lepanthes edwardsii Ames	H
	Lepanthes johnsonii Ames	H
	Lepanthes vilchezii F.L. Archila	H
	Lepanthes s p. 1 (S.B.)	H
	Lycaste deppei (Lodd.) Lindl.	H
	Maxillaria aff. *biolleyi* (Schltr.) L.O. Williams	H
	Maxillaria cucullata Lindl.	H
	Maxillaria histrionicum (Rchb. f.) L.O. Williams	H
	Maxillaria neglecta (Schltr.) L.O. Williams	H
	Nidema boothii (Lindl.) Schltr.	H
	Oncidium cf. *graminifolium* (Lindl.) Lindl.	H
	Oncidium sphacelatum Lindl.	H
	Oncidium s p. 1 (S.B.)	H
	Pleurothallis broadwayi Ames	H
	Pleurothallis cardiothallis Rchb. F.	H
	Pleurothallis dolichopus Schltr.	H
	Pleurothallis grobyi Batem. ex Lindl.	H
	Pleurothallis matudana C. Schweinf.	H

Table A2.1 *Cont.*

Family	Species	Life-form
Orchidaceae (*cont*.)	*Pleurothallis segoviensis* Rchb.f.	H
	Pleurothallis tuerckheimii Schltr.	H
	Pleurothallis s p. 1 (S.B.)	H
	Pleurothallis sp.2 (D.K.)	H
	Prosthechea ochracea (Lindl.) W.E. Higgins	H
	Prosthechea pygmaea (Hook.) W.E. Higgins	H
	Prosthechea rhynchophora (A. Rich. & Galeotti) W.E. Higgins	H
	Prosthechea vitellina (Lindl.) W.E. Higgins	H
	Rhynchostele cordata (Lindl.) Soto Arenas & Salazar	H
	Scaphyglottis confusa (Schltr.) Ames & Correll	H
	Scaphyglottis fasciculata Hook.	H
	Sobralia macrantha Lindley	H
	Sobralia xantholeuca Hort. ex Williams	H
	Stelis aprica Lindl.	H
	Stelis cf. *hirsuta* (Garay) Garay	H
	Stelis cf. *parvula* Lindl.	H
	Stelis guatemalensis Schltr.	H
	Stelis immersa (Linden & Rchb. F.) Pridgeon & M.W. Chase	H
	Stelis villosa (Knowles & Westc.) Pridgeon & M.W. Chase	H
	Stelis s p. 1 (S.B.)	H
	Stelis s p. 2 (S.B.)	H
	Stenostyla lendyana (Reichb. f.)	H
	Trichosalpinx s p. 1 (S.B.)	H
Passifloraceae		
	Passiflora hahnii (E. Fourn.) Mast.	C
	Passiflora membranacea Benth.	C
	Passiflora sexflora Juss.	C
Piperaceae		
	Peperomia deppeana Schltdl. & Cham.	Ph
	Peperomia glabella (Sw.) A. Dietr.	Ph
	Peperomia tenella (Sw.) A. Dietr.	Ph
	Peperomia s p. 1 (S.B.)	Ph
	Peperomia s p. 2 (S.B.)	Ph
	Piper aff. *ottoniifolium* C. DC.	C
Polygalaceae		
	Securidaca cf. *diversifolia* (L.) S.F. Blake	C
Polypodiaceae		
	Campyloneurum angustifolium (Sw.) Fée	H
	Cochlidium rostratum (Hook.) Maxon ex C. Chr.	H
	Lellingeria delitescens (Maxon) A.R. Sm. & R.C. Moran	H
	Lellingeria delitescens (Maxon) A.R. Sm. & R.C. Moran	H
	Melpomene anfractuosa (Kunz ex Klotzsch) A.R. Sm. & R.C.	H
	Melpomene xiphopteroides (Liebm. A.R. Sm. & R.C. Moran)	H
	Microgramma percussa (Cav.) De la Sota	H
	Microgramma sp.1 (D.K.)	H
	Micropolypodium trichomanoides (Sw.) A.R. Sm	H

Table A2.1 *Cont.*

Family	Species	Life-form
Polypodiaceae (*cont.*)	*Niphidium crassifolium* (L.) Lellinger	H
	Pecluma alfredii (Rosenst.) M.G. Price	H
	Phlebodium pseudoaureum (Cav.) Lellinger	H
	Pleopeltis angusta Humb. & Bonpl. ex Willd.	H
	Pleopeltis astrolepis (Liebm.) E. Fourn.	H
	Pleopeltis crassinervata (Fée) T. Moore	H
	Pleopeltis macrocarpa var. *macrocarpa* (Bory ex Willd.) Kaulf.	H
	Pleopeltis mexicana (Fee) Mickel & Beitel	H
	Polypodium echinolepis Fee	H
	Polypodium furfuraceum Schltdl. & Cham.	H
	Polypodium hartwegianum Hook.	H
	Polypodium longepinnulatum Fourn.	H
	Polypodium plebeium Schltdl. & Cham.	H
	Polypodium plesiosorum Kunze	H
	Polypodium polypodioides var. *aciculare* Weath.	H
	Polypodium polypodioides var. *polypodioides* (L.) Watt	H
	Polypodium puberulum Schltdl. & Cham.	H
	Polypodium s p. 1 (S.B.)	H
	cf. *Polypodium s* p. 2 (S.B.)	H
	Serpocaulon aff. *dissimile*	H
	Serpocaulon lasiopus (Klotzsch) A.R. Sm.	H
	Serpocaulon triseriale (Sw.) A.R. Sm.	H
Pteridaceae		
	Vittaria graminifolia Kaulf.	H
	Vittaria s p. 1 (S.B.)	H
Rosaceae		
	Rubus alpinus Macfad.	C
Rubiaceae		
	Cosmibuena matudae (Standl.) L.O. Williams	Ph
	Galium hypocarpium (L.) Endl. ex Griseb.	C
	Hoffmannia cf. *excelsa* (Kunth) K. Schum.	C
	Sabicea villosa Roem. & Schult	C
Rutaceae		
	Zanthoxylum foliolosum J.D. Sm.	C
Santalaceae		
	Antidaphne hondurensis Kuijt	P
	Antidaphne viscoidea Poepp. & Endl.	P
	Arceuthobium vaginatum (H.B.K.) Eichler	P
	Dendrophthora squamigera (Benth.) Kuntze	P
	Dendrophthora sp. 1 (D.K.)	P
	Dendrophthora sp. 2 (D.K.)	P
	Phoradendron cf. quadrangulare (HBK) Krug & Urb.	P
	Phoradendron nitens Kuijt	P
	Phoradendron piperoides (HBK) Trel.	P
	Phoradendron undulatum (Pohl) Eichler	P

Table A2.1 ***Cont.***

Family	Species	Life-form
Sapindaceae		
	Paullinia cf. *serjaniifolia* Triana & Planch.	C
	Serjania rhachiptera Radlk.	C
Selaginellaceae		
	Selaginella schizobasis Baker	H
	Selaginella stellata Spring	H
Schlegeliaceae		
	Schlegelia cf. *spruceana* Bureau & K. Schum.	C
Smilacaceae		
	Smilax domingensis Willd.	C
	Smilax spinosa Mill.	C
	Smilax subpubescens A.DC.	C
	Smilax sp. 1 (D.K.)	C
Solanaceae		
	Cestrum sp. 1 (D.K.)	C
	Lycianthes chiapensis (Brandegee) Standl.	C
	Lycianthes lenta (Cav.) Bitter	C
	Lycianthes nitida Bitter	C
	Merinthopodium neuranthum (Hemsl.) Donn. Sm.	C
	Solanum nudum Dunal	C
	Witheringia solanacea L' Herit.	C
Verbenaceae		
	Aegiphila quararibeana Rueda	C
Vitaceae		
	Cissus cacuminis Standl.	C
	Cissus trifoliata (L.) L.	C
	Cissus aff. *sicyoides* L.	C
	Cissus s p. 1 (S.B.)	C
	Vitis tiliifolia Humb. & Bonpl. ex Schult.	C
	Vitis sp. 1 (S.B.)	C
unknown		
	Climber 6 (S.B.)	C
	Climber 7 (S.B.)	C
	Climber 8 (S.B.)	C
	Hemi-epiphyte sp. 1 (S.B.)	Ph

Appendix 3. Batke S.P. and Hill N. (2013) First Record of *Serpocaulon lasiopus* (Polypodiaceae) from Mesoamerica. American Fern Journal 103:182-184.

Serpocaulon has been recently segregated from *Polypodium* by Alan Smith and colleagues (Smith et al. 2006). The genus is entirely neotropical or subtropical in distribution, with 40 species occurring only in South America. One of its species is *S. lasiopus* (Klotzsch) A. R. Sm. [basionym: *Polypodium lasiopus* (Klotzsch 1847)], whose geographic distribution according to Smith et al. (2006) is Venezuela, Ecuador, Peru, and Bolivia. Specimens of *S. lasiopus* not seen by Smith et al. (2006) were also recently found in Colombia (Idárraga-Piedrahita et al. 2011), Argentina (A. Paul *pers. com.*, 2013), Haiti (A. Paul *pers. com.*, 2013) and the Dominican Republic (TROPICOS). The species was not treated in *Flora Mesoamericana* (Davidse et al. 1995), nor has it been reported in the more recent fern volume for the *Flora of Nicaragua* (Stevens et al. 2009).

In 2012 during an epiphyte survey in Cusuco National Park, Honduras ($15^0$32'31"N and $88^0$15'49"W), as part of the first author's Ph.D. research, two small populations of *S. lasiopus* were found in moist broad-leaved mountain forest in the Sierra de Merendón west of San Pedro Sula. The specimens were identified by Alan R. Smith (UC). The first population of *S. lasiopus* was collected 35 m above ground on a large mature tree of *Liquidambar styraciflua* L. (1903 m asl.). The second population was collected at 18 m above ground on a large mature tree of *Ilex pallida* Standl (1877 m asl.). Both populations consisted of fertile individuals but with less than 10 individuals on each tree. The specimens were deposited at Trinity College Dublin with one duplicate at UC. Another duplicate will also be transferred to the herbarium in UNAH (TEFH). The specimens are the first documentation of *S. lasiopus* in Mesoamerica (i.e., Honduras). The fact that *S. lasiopus* has not been previously reported from Mesoamerica is probably because, at least in Honduras, it grows as a canopy epiphyte, making it difficult to detect. Also, there has been little research on epiphytes in Honduras.

In *Flora Mesoamericana*, *S. lasiopus* falls within the *Polypodium loriceum* Group 2 (Davidse et al. 1995), which was grouped by Smith et al. (2006) within the *P. loriceum*, *P. fraxinifolium* and allies Group 7. This group is distinctive by long-creeping rhizomes that bear partially or entirely clathrate, brownish or blackish scales. According to *Flora Mesoamericana* and *Flora of Nicaragua*, *S. lasiopus* would key out to the *P. dissimile* and/or *P. wagneri section*. What distinguishes *S. lasiopus* from these species are characters of venation, blade dissection, and indument (septate scales/hairs). This species can be distinguished from other *Serpocaulon* species within the *Flora Mesoamericana* by having moderately to dense indumenta on both sides of the pinna consisting of 4–7 tricomes cells and rhizome scales that are 0.4–0.6 cm long (as opposed to 0.6–1.1 cm in the case of *S. dissimile* (L.) A.R. Sm. and 0.2–0.3 cm in the case of *S. wagneri* (Mett.) A.R. Sm.).

The stems of *S. lasiopus* are creeping, thick, fleshy, fragile, scales lanceolate, long-acuminate, margin scabrous, shiny, dirty brown and glabrous. Leaves are pinnatifid, sublanceolate, attenuate towards the apex, remote and minutely viscid-pubescent on both sides. The lobes are oblong, obtuse, membranous, approximate, horizontal and weakly deflexed. Rachis and stipe are generally markedly pale yellow and minutely viscid-pubescent on both sides. Older sori are uniseriate and pale yellow. The leaf blades on our specimens are approximately 4.5 cm long and 0.6 cm wide, but they have previously been recorded as long as 7.6–10.2 cm and as wide as 3.2–3.9 cm (Klotzsch 1847). The sori are 0.8–2.2 mm wide. The stipes are slender and approximately 12.5 cm long. We provide an illustration of this plant (Figure A3.1) because, to our knowledge, it has not been previously illustrated.

This note is one of the results of a Ph.D. project that aims to provide a preliminary list of epiphytes in Cusuco National Park and to assess their ecology and distribution within it. The project is supported by Trinity College Dublin, the Rufford Foundation and Operation Wallacea. We thank Sarah Willis for preparing the drawings, Dr. Daniel L. Kelly for his supervision and Dr. Alan R. Smith (UC) for the species determination.

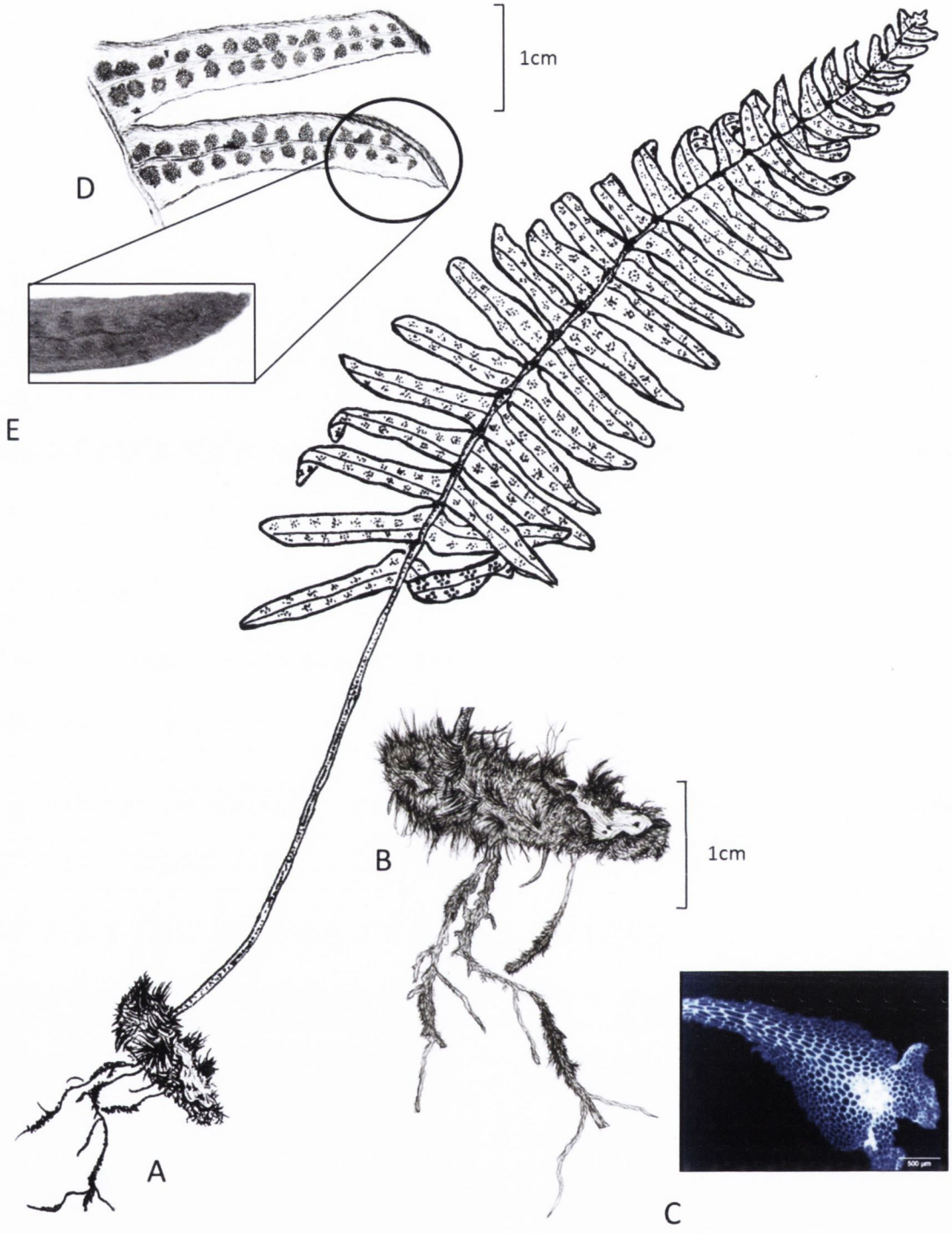


Figure A3.1 A–E *Serpocaulon lasiopus*. A. Habit. B. Rhizome. C. Detail of the rhizome scale. D. Abaxial surface detail of pinna with sori. E. Indument on pinna. Drawings provided by Sarah Willis.

Appendix 4.

Table A4.1 Mechanically dependent plant NMS ordination axis scores at a plot level, correlated to environmental variables using Spearman's rank correlation coefficient. Individual plots were used as a sampling unit and an ordination was run at a community levels (individual species). A Sørensen (Bray-Curtis) distance measure was used to identify the percent of variance in the distance matrix for each axis (R^2). Only coefficient values that were significant are shown ($P < 0.05$). ns = non-significant. NMS stress value for the community ordination = 2.84.

Plot (n = 10)			
		Axis1	Axis2
Variance explained (R^2)		0.90	0.70
	Mean VPD	-0.94	ns
	Elevation	0.85	ns
	Aspect	-0.80	ns
	Slope	ns	-0.69
	Exposure	ns	ns

Figure A4.1 3-dimensional NMS ordination comparing the floristic affinities among angiosperm epiphytic floras across Central America. A Sørensen (Bray-Curtis) distance measure was used. NMS stress value for the ordination = 6.38.

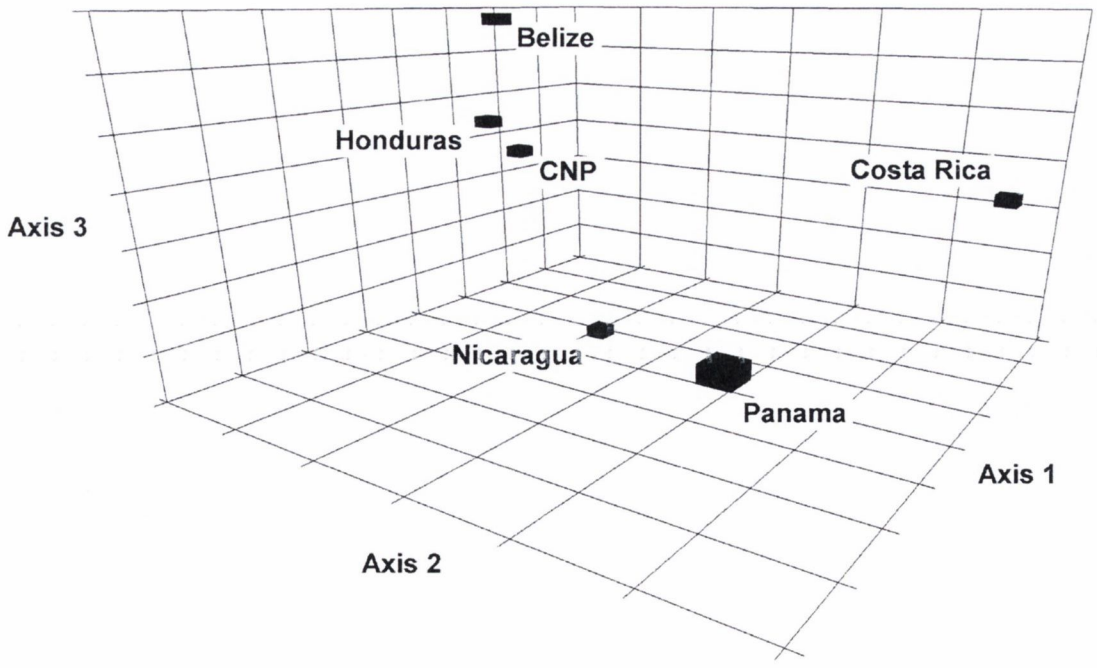


Table A4.2 Mechanically dependent plant NMS ordination axis scores at a tree level, correlated to environmental variables using Spearman's rank correlation coefficient. Individual trees were used as a sampling unit and ordinations were run at a community level. A Sørensen (Bray-Curtis) distance measure was used to identify the percent of variance in the distance matrix for each axis (R^2). Only coefficient values that were significant are shown ($P < 0.05$). ns = non-significant. NMS stress value for the community ordination for trees located at low elevation sites = 11.49; and high elevation sites = 14.92.

Level	**Variables**	**Community**	
Tree (n = 60)			
		Axis1	Axis2
Low elevation (n = 30)			
Variance explained (R^2)		0.59	0.26
	Canopy openness	ns	-0.73
	EVSS (SE)	-0.83	ns
	Tree type	-0.53	-0.35
	Tree circumference	ns	-0.53
	Tree height	ns	-0.46
	Tree surface area	-0.40	ns
	EVSS (S)	-0.46	ns
	Canopy extent (N)	ns	-0.55
	Canopy extent (W)	ns	ns
	Canopy extent (S)	ns	ns
	Canopy extent (E)	ns	ns
High elevation (n = 30)			
Varance explained (R^2)		0.60	0.22
	Canopy openness	0.42	0.61
	EVSS (S)	ns	0.65
	Tree height	-0.46	0.60
	Tree surface area	ns	0.61
	EVSS (SE)	ns	0.59
	Tree circumference	ns	0.54
	Tree type	ns	0.51
	Canopy extent (N)	ns	ns
	Canopy extent (W)	ns	ns
	Canopy extent (S)	ns	ns
	Canopy extent (E)	ns	ns

Table A4.3 Mechanically dependent plant NMS ordination axis scores at a branch level, correlated to environmental variables using Spearman's rank correlation coefficient. Individual branches were used as a sampling unit and two separate ordinations were run, at life-form and family level. A Sørensen (Bray-Curtis) distance measure was used to identify the percent of variance in the distance matrix for each axis (R^2). Only coefficient values that were significant are shown ($P < 0.05$). ns = non-significant. NMS stress value for the family ordination = 12.5; and the life-form ordination = 6.1.

Level		**Family**			**Life-form**	
Branch (n = 1108)						
		Axis1	Axis2	Axis3	Axis1	Axis2
Variance explained (R^2)		0.44	0.25	0.22	0.90	0.80
	Branch surface area	0.15	0.39	-0.20	-0.46	ns
	Bryophyte cover	0.23	0.34	0.24	-0.21	-0.18
	Lichen cover	0.07	-0.32	ns	0.31	ns
	Bark roughness	0.29	0.15	ns	-0.19	ns
	Bark flakiness	-0.21	-0.08	ns	0.09	0.16
	Branch inclination	ns	-0.05	0.17	0.13	ns
	Bark fissuring	ns	ns	-0.15	-0.19	ns
	Branch aspect	ns	ns	ns	ns	ns

Table A4.4 Summary of the mechanically dependent plant NMS ordinations. The percentage of variance that was explained by environmental variables and geographical distance are summaries at a plot, tree and branch level. Mantel tests with Sørensen (Bray-Curtis) distance measure were used for the analysis.

Level	**Environmental variance (%)**	**Geographic variance (%)**	**Total variance (%)**
Plot	44.4	46.3	90.7
Tree	6.8	41.6	48.4
Low elevation	30.0	nd	30.0
High elevation	30.1	nd	30.1
Branch	18.9	nd	18.9