

**Nowhere to escape – Diversity and community composition
of ferns and lycophytes on the highest mountain in
Honduras**

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6 **and lycophytes on the highest mountain in Honduras**
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31 **Running title:** Fern diversity along altitudinal gradient in Honduras
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35 **Keywords:** Altitudinal gradients, Celaque, Central America, Climate change, Cloud forest,
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37 Epiphytes, Mid-elevation peak, Species richness
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Abstract

IPCC predictions for Honduras indicate that temperature will increase by up to 3-6°C and precipitation will decrease by up to 7-13% by the year 2050. To better understand how fern and lycophyte communities might be affected by climate change, we comprehensively surveyed the community compositions of ferns and lycophytes at Celaque National Park, the highest mountain in Honduras. We surveyed a total of 80 20x20m² plots along an altitudinal gradient of 1249-2844m a.s.l., identifying all species and estimating their abundances. We recorded a total of 11,098 individuals from 160 species and 61 genera. Community composition was strongly influenced by changes in altitude, precipitation, and the abundance of bryophytes (a proxy for air humidity). Of the 160 species, 63 are expected, under a RCP2.6 scenario for the year 2050, to shift their range fully or partially above the maximum altitude of the mountain. Of these, 65.1% are epiphytes. We found that species with narrow altitudinal ranges at high altitudes were more at risk. Our study indicated that conservation efforts should prioritise higher altitudinal sites; focusing particularly on preserving the vulnerable epiphytic fern species, which are likely to be at greater risk.

Introduction

Mountains are ideally suited to study the effect of climate change on species distributions due to their rapid variability of climate over short altitudinal distances (Kessler *et al.* 2016, Rogora *et al.* 2018). In addition, these geographic features often harbour a very diverse and unique assemblage of fauna and flora and form regional biodiversity hotspots of high conservation importance (Lomolino 2001). Many of these species have discrete altitudinal distributions, determined partially by their biology and the historical distribution of each species, amongst other factors (Watkins *et al.* 2006). Current evidence suggests that plant species ranges have seen an average increase of approximately 30-36m upwards along altitudinal gradients over

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3 the last 10 years, an affect that can be attributed to climate change (Jump *et al.* 2012, Lenoir *et*
4 *al.* 2008, Morueta-Holme *et al.* 2015). Projections suggest that under a 1.5°C increase scenario
5
6 we can anticipate further upward shifts in altitude and a loss of >50% of the geographic range
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8 of 8% of plant species by the year 2030 (IPCC 2018). Tropical locations, in particular, are
9
10 believed to show exacerbated effects of climate change on altitudinal distribution patterns,
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12 largely due to the narrow optimal temperature ranges of tropical species (Feeley & Silman
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14 2010), with beneficial effects for some species and detrimental results for others (Gibson-
15
16 Reinemer & Rahel 2015).

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21 Upslope shifts have potentially negative implications for future diversity, by increasing the risk
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23 of extinction for species that occupy high altitude sites and that have a narrower range size
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25 (Colwell *et al.* 2008). As such, altitudinal distribution patterns have been studied for several
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27 decades, with particular focus on tropical forest vegetation (Cardelus *et al.* 2006, Ibisch *et al.*
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29 1996, Kessler 2001, Kidane *et al.* 2019, Krömer *et al.* 2005, Rahbek 1995, Richards 1952, Wolf
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31 1993, Zhou *et al.* 2019). However, many Central and South American studies have mostly
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33 focused on countries such as Costa Rica (Stroud & Feeley 2017), whilst other areas, including
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35 Honduras, have been largely neglected, making generalisations on the effect of climate change
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37 on species altitudinal distributions difficult. In particular, the limited attention that Honduras
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39 has received has also been restricted to a small number of taxonomic groups. The greatest
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41 concentration of these studies in Honduras has focused on birds (Jones *et al.* 2020, Neate-Clegg
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43 *et al.* 2018), with fewer studies investigating invertebrates (Anderson & Ashe 2000) and plants
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45 (Imbach *et al.* 2013).

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52 Ferns and lycophytes are especially vulnerable to increased temperatures and decreased
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54 precipitation, which are both predicted under future climate change, and their responses to these
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56 conditions will likely differ between terrestrial and epiphytic species (Mandl *et al.* 2010). As a
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58 result, this climate sensitive, globally distributed and diverse group of plants, has received
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3 substantial attention in the literature on global altitudinal distribution pattern studies; both
4 directly (Kessler *et al.* 2001, Kluge & Kessler 2011, Mandl *et al.* 2010, Watkins *et al.* 2006)
5 and indirectly (Sánchez-González *et al.* 2010). However, there is still a severe lack of available
6 distribution data for ferns and lycophytes from some Central American countries such as
7 Honduras, and there is currently no specific distributional data available for epiphytic ferns and
8 lycophytes from anywhere in Honduras. For example, epiphytes until now have only been
9 exclusively studied in Honduras in the context of disturbance events (Batke & Kelly 2015) and
10 biogeographical comparisons (Batke *et al.* 2016). This is a concerning realisation when
11 considering that Honduras contains a high percentage of vascular epiphytes relative to the
12 overall flora of the country (e.g. >30% of 908 vascular plant species in Cusuco National Park),
13 and compared to other Central America countries (Batke *et al.* 2016).

14
15 In contrast to the geographical limitations of plant altitudinal distribution research in Honduras,
16 the theory behind the migration of plants upwards along altitudinal gradients has been well-
17 established elsewhere. It is believed that climate warming offers more optimal conditions that
18 favour the establishment and survival of plant species at the upper limits of their temperature
19 ranges (Adams & Kolb 2005); effectively resulting in an upslope 'march'. Other theories have
20 also been used to explain upslope plant shifts, such as the synchronous 'lean' response,
21 although these hypotheses are not mutually exclusive and may occur in sequence or
22 combination (Breshears *et al.* 2008). However, the individual response of particular plant
23 groups has been shown to vary greatly (Grau *et al.* 2007, Grau *et al.* 2011, Wolf *et al.* 2016).
24 For example, epiphytes, which are restricted to life in the canopy, are often separated from the
25 terrestrial soil environment (Zotz & Hietz 2001, Zotz *et al.* 2001) and have been suggested to
26 therefore respond very differently compared to terrestrial plants (Nervo *et al.* 2019);
27 particularly as epiphytes are also highly sensitive to changing climate conditions (Ellis 2013,
28 Ellis & Coppins 2007, Ellis & Coppins 2009, Ellis & Coppins 2010, Hsu *et al.* 2012, Zotz &
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3 Bader 2009). Thus, the lack of altitudinal distribution data on terrestrial and epiphytic ferns
4 and lycophytes from Honduras, currently prevents us to compare plant distributional responses
5 to predicted changes in future climate to other biodiversity hotspots (Marchese 2015, Myers *et*
6 *al.* 2000).
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13 To improve our understanding of fern community assemblages across the greatest altitudinal
14 range in Honduras, in this study we (1) investigated for the first time how species richness,
15 diversity and community composition patterns of ferns and lycophytes changes along an
16 altitudinal gradient on the highest mountain in Honduras, (2) tested whether there are
17 differences within these patterns between epiphytes and terrestrial species, (3) attempted to
18 identify the underlying environmental factors that drive these patterns, and (4) identified which
19 species are likely to be at greater risk under predicted changes in climate. It is hoped that the
20 data from this study can help us to better understand and generalise the effect of future changes
21 in climate on plant distributions in tropical mountain forests.
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36 **Methods**

37 *Study site*

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42 Celaque Mountain National Park (14°32'08"N, 88°42'26"W) is located within the western
43 region of Honduras, between the departments of Copán, Lempira and Ocotepeque (Figure. 1).
44 The term 'Celaque' comes from the Lenca word "Celac", which means "cold water" or "ice
45 water" and is a reference to the large quantity of flowing water in the park (Flores *et al.* 2012).
46 The protected area contains the highest mountain in Honduras, with an altitude of 2849m above
47 sea level (a.s.l.).
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57 The topography in Celaque is rugged with sandy and shallow soils (Archaga 1998). The
58 vegetation community classification has not been well defined, but it has been broadly
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3 described as *Pinus-Quercus* (pine-oak) forest at lower altitude and transitional mixed broad-
4 leaf/pine montane forest at middle to upper altitude. Above 2200m the transitional forest gives
5 way to mainly broadleaved species (Archaga 1998, Southworth *et al.* 2004). Celaque is
6 believed to be one of the most biologically important sites for plants in Honduras, due to its
7 high degree of endemism and diversity (Hermes *et al.* 2016, ICF 2016). With 217 species
8 recorded to date, ferns species are particularly abundant in Celaque. It is believed to be the
9 most species rich nature reserve in the country for this group (Chávez *et al.* 2020, Reyes-
10 Chávez *et al.* 2018, Rojas-Alvarado 2012, Rojas-Alvarado 2017), with two of the seven known
11 Honduran endemic fern species occurring there.
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26 *Plot selection*

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29 We surveyed a total of 80 20x20m² (400m²) plots between August 2018 and July 2019, along
30 an altitudinal gradient of 1595m (1249-2844m a.s.l) (Figure 1). Every 100m in altitude, we
31 selected five plots using a stratified random design, focusing on the most representative forest
32 types including ravines and riparian zones, but excluding canopy gaps, landslides, or other
33 highly disturbed areas where possible. Between 2200m and 2400m, the topography of Celaque
34 was very steep (an approximate slope of 60%), which made it unsafe to sample plots at 2300m.
35
36 In each plot, we surveyed fern and lycophyte richness and abundance (by counting every
37 individual in each plot) following Kessler & Bach (1999) and Karger *et al.* (2014). For species
38 with long rhizomes, individuals were counted by identifying clumps, which most likely
39 represented genets. We collected epiphytes by searching for low hanging individuals or fallen
40 branches, as well as a visual search using binoculars from a suitable vantage point.
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55 We identified all ferns and lycophytes to species. Where necessary, we collected voucher
56 specimens for further analysis and verification. In the case of the genus *Elaphoglossum* Schott
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3 ex J. Sm., we collected a sample of each morphospecies for closer laboratory examination and
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5 counted the number of each type found in each plot.
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8 For each plot we measured inclination using a clinometer and estimated the amount of soil
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10 covered by plants or rocks and total cover of bryophytes on canopy branches as a proxy for air
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12 humidity (Karger *et al.* 2012). Percentage soil covered by plants or rocks and total bryophyte
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14 cover were visually estimated in the field to the nearest 5%. All estimations were carried out
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16 by the same individual.
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20 All the samples were deposited at EAP herbarium of Zamorano University, Honduras.
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22 Collections were identified using *Flora Mesoamericana* (Moran 1997), *The Pteridophytes of*
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24 *Mexico* (Mickel & Smith 2004) and other relevant publications (Gonzales & Kessler 2011,
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26 Rojas-Alvarado 2003). We followed PPGI (2016) and Hassler & Schmitt (2020) for species
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28 classification.
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32 33 34 35 *Data analysis*

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37 A digital elevation model (DEM) of the park was created using a 50m contour map. The model
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39 was created using scene in ArcGIS 10.8 (ESRI 2020).
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43 The community data was visualised using Nonmetric Multidimensional Scaling (NMS) and
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45 Simpson diversity was calculated with the R ‘vegan’ package (R Developing Core Team 2020).
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47 To identify the most important response variable that affected Simpson diversity and
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49 fern/lycophyte community composition in Celaque, the Simpson diversity and NMS
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51 community scores were correlated in a random/mixed-effects meta-regression model with all
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53 response variables. We used the ‘glmulti’ package in R for this analysis (R Developing Core
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55 Team 2020). We fitted the meta-regression model separately for NMS axis 1 and 2. In addition,
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57 Simpson diversity was also separately fitted for epiphyte and terrestrial species. The relative
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3 model average importance of each variable was plotted and the best-fit model selected using
4 Akaike's Information Criterion (AIC) (Batke & Kelly 2014). We used a 0.8 cut-off to
5 differentiate between important and less important variables (Calcagno & de Mazancourt
6 2010). In order to assess the richness distribution of terrestrial and epiphytic species along an
7 altitudinal gradient, a spline regression was fitted with a series of polynomial segments using
8 R (Bruce *et al.* 2020, R Developing Core Team 2020).
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11 We extracted current temperature and precipitation data for Celaque from Karger *et al.* (2017)
12 and climate predictions for temperature and precipitation for western Honduras for the years
13 2050 and 2100 for RCP2.6 and RCP8.5 from the *Fifth Assessment Report* (IPCC 2014). To
14 assess altitudinal shifts, as expected from warming and decreases in precipitation, we
15 calculated the lapse rates following Burt & Holden (2010). For each species, we used the
16 rearranged fitted linear equations for the temperature and quadratic equations for the
17 precipitation projections (i.e. solving for x), to calculate altitudinal changes for temperature
18 and precipitation of each climate scenario and year respectively. We then calculated the number
19 of species that lost all or some of their altitudinal range for each year and climate change
20 scenario. A full loss of range was defined when the minimum altitude of a given species
21 exceeded that of the highest point of the mountain (i.e. 2849m).
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45 **Results**

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47 We recorded a total of 11,098 individual ferns and lycophytes from 160 species and 61 genera
48 (Supplementary Material - Table 1). Of the 11,098 individuals, 7,036 were epiphytes (78
49 species) and 4,062 were terrestrial plants (82 species). The five species with the highest
50 abundance were *Elaphoglossum latifolium* (Sw.) J. Sm. (527 individuals), *Blechnum*
51 *occidentale* L. (394 individuals), *Niphidium crassifolium* (L.) Lellinger (393 individuals),
52 *Pecluma dulcis* (Poir.) F.C. Assis & Salino (370 individuals) and *Polypodium fissidens* Maxon
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3 (361 individuals). When analysing both life-forms together, species richness were highest at
4 high altitudinal sites (~2000 - 2600m) (Figure 2A). The same pattern was found for epiphytes
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6 whereas terrestrial species had highest richness around ~2000m, showing a hump-shaped
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8 relationship with altitude (Figure 2A).
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13 Current altitudinal range sizes did not differ significantly between epiphytes and terrestrial
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15 plants ($p>0.05$). However, range sizes were proportionally smaller at low and high altitudinal
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17 sites compared to middle altitudinal sites (not shown).
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21 Community composition in Celaque National Park was strongly influenced by changes in
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23 altitude. Higher altitude sites were floristically different compared to low altitude sites. An
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25 NMS ordination (stress = 0.19) clearly illustrated a transitional change in community similarity
26
27 along axis 1 (Figure 2B), which was strongly driven by altitude, bryophyte cover and
28
29 precipitation (Figure 3A & B; Table 1).
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33 Similarly, Simpson diversity for epiphytes positively correlated to a high abundance of
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35 bryophytes, low cover of ground vegetation and low temperatures. It needs to be noted that
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37 although ground vegetation cover was an important model factor, it was non-significant for the
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39 best-fit model (Figure 3C; Table 1). Terrestrial species diversity on the other hand were
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41 positively correlated to high rain fall, high bryophyte cover and low canopy height, however,
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43 only precipitation was statistically significant in the best-fit model for terrestrial species (Figure
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45 3D; Table 1). Bryophyte cover was positively correlated with altitude ($F=14.22$, $R^2\text{-adj}=0.55$,
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47 $p<0.01$).
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52 Based on IPCC predictions for western Honduras, we are expected to see a temperature
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54 increase between 3-6 °C and a precipitation decrease between 7-13% (Figure 4). Of the 160
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56 species identified, between 7 and 32 species are expected to shift their ranges above the
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58 maximum altitude (2849m) of the highest mountain in Honduras (Supplementary Material
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3 Table 1; Table 2; Figure 5). Generally, epiphytes were more negatively affected at high
4 altitudinal sites compared to terrestrial species due to their narrower range sizes at high altitude
5 and negative association with higher air temperatures (Table 1; Figure 3C). The percentage
6 mean altitudinal range lost was between 10-18% higher in epiphytes compared to terrestrial
7 ferns. For example, of the eight known Hymenophyllaceae Mart. (filmy ferns) epiphytes found
8 in this study, four would lose 100% of their suitable habitat range, whereas another two would
9 lose between 9-87% of their range.
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23 Discussion

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26 There has been limited research into the altitudinal distribution patterns of epiphytic and
27 terrestrial fern and lycophytes along mountain ranges, especially in the context of climate
28 change. To our knowledge, our study is the first to explore these changing patterns in Honduras.
29 Understanding plant distribution patterns and identifying the most vulnerable species under
30 future predicted change in climate along altitudinal gradients is important, as it has been shown
31 that high altitude species are particularly vulnerable under rising atmospheric temperatures
32 (Freeman *et al.* 2018). Increased atmospheric temperatures and decreased water availability
33 from changes in precipitation and cloud formation, has been suggested to exacerbate species
34 losses in high altitudinal sites (Still *et al.* 1999), due to a loss in suitable habitat conditions for
35 those species that have a small-high altitudinal range. These changes in climate are particularly
36 relevant to mountain systems, which exhibit rapid changes in environmental conditions across
37 an altitudinal gradient (Rogora *et al.* 2018), relative to their specific geographic region (Kessler
38 *et al.* 2016), with evidence to suggest that mountains offer an ‘elevator to extinction’ for high
39 elevation species (Freeman *et al.* 2018).
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3 Previous studies that investigated the effect of climate change on plant distributions in
4 mountains have often focused on non-tropical mountain biomes, including temperate (Allen &
5 Lendemer 2016, Janssen *et al.* 2019), Mediterranean (Di Nuzzo *et al.* 2021), alpine (Saiz *et al.*
6 2021) and subtropical localities (Song *et al.* 2012). Fewer studies have specifically focused on
7 tropical locations (Acevedo *et al.* 2020, Hsu *et al.* 2014, Pouteau *et al.* 2016), and with even
8 less data are available for biodiversity hotspots in Central or South America (Acevedo *et al.*
9 2020). In addition, the altitudinal distribution of selected groups of epiphytes in these
10 understudied tropical montane regions; specifically for epiphytic ferns and lycophytes, remain
11 vastly under-explored (Pouteau *et al.* 2016), making comparisons difficult between Honduras
12 and other localities.
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15 We document here, for the first time, the altitudinal distribution patterns of epiphytic and
16 terrestrial ferns in Honduras- along the highest mountain in this country. Our study shows that
17 epiphytes along this mountain exhibit small-high altitudinal ranges. This narrow range has
18 important implications for epiphyte survival; resulting in a greater risk of extinction under
19 future predicted changes in climate, as the ranges of some of these species are likely to shift
20 beyond the maximum elevation of the mountain. For instance, we found that, although species
21 of both epiphytic and terrestrial life-forms with narrow range sizes are at high risk in Celaque
22 NP under future IPCC predictions for Honduras, epiphytes were more vulnerable. This is
23 attributed to the higher species richness and abundance of epiphytes at high altitude plots (ca.
24 2466-2866m) under current climate conditions, compared to terrestrial species, which had a
25 higher abundance and richness at mid-altitude. As a result, of the 63 species identified to be at
26 risk (partial or total loss of range) under RCP2.6 for the year 2050, 65.1% were epiphytic taxa,
27 despite epiphytes making up less than 50% of all species recorded. The higher richness in
28 epiphytes at high elevation sites is thus likely to make them more vulnerable to change in
29 climate conditions, due to their differences in response to environmental conditions compared
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3 to terrestrial species (Benzing 1990) and their closer range-proximity to the maximum
4 elevation of the mountain. Similar results were reported from studies on other vascular and
5 non-vascular species (Zotz & Bader 2009). For instance, many epiphytic ferns are anchored in
6 the forest canopy with no direct connection to the terrestrial soil environment; relying on dead
7 organic canopy matter for nutrients and rain or atmospheric water vapour for moisture input
8 (Benzing 1998, Foster 2001, Hsu *et al.* 2014, Zotz & Bader 2009). Terrestrial species on the
9 other hand are intimately connected to the forest soil through their root system and thus rely
10 much less on atmospheric moisture and canopy organic substrata for their water requirements
11 and nutrient uptake.
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24 Our study demonstrated that 7-31 species of lycophytes and ferns are likely to lose 100% of
25 their range between 2050 and 2100. Epiphytic ferns, however, are likely to have a higher loss
26 of species compared to terrestrial ferns, due to their higher predicted range loss (i.e. 10-18%
27 more than terrestrial species). Global simulation of 2°C increase in temperature by 2100, has
28 been predicted to result in the loss of over half the range of 16%-57% of plant species (Smith
29 *et al.* 2018, Warren *et al.* 2018), suggesting that our findings are for some species above the
30 global average. We found that particularly, epiphytic ferns that require a continuous water
31 supply, such as species of the genus *Hymenophyllum* Sm. (Hymenophyllaceae), are predicted
32 to be of greater risk. *Hymenophyllum* species are found abundantly in humid tropical forests
33 and have been characterised as shade plants, which are well adapted to low light but require
34 ample water supply (Evans 1964, Richards & Evans 1972). These species are considered good
35 indicators of high atmospheric humidity (Hietz & Hietz-Seifert 1995) and due to their
36 dependency on moist habitats, are extremely sensitive to water loss because of their single layer
37 cell structure and lack of a well-developed cuticle and stomata (Proctor 2003).
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56 The higher species richness of epiphytes at a higher altitude in Honduras, is likely the result of
57 increased precipitation and more continuous water supply (McAdam & Brodribb 2012, Nervo
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3 *et al.* 2019). Epiphytic species that are sensitive to water availability appeared to favour higher
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5 altitudinal sites, with lower temperature conditions, increased cloud formation and a supply of
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7 fine and frequent precipitation compared to low altitudinal sites (Bhattarai *et al.* 2004, Frahm
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9 & Gradstein 1991). This was demonstrated by the change in community composition along the
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11 altitudinal gradient, with a higher prevalence of epiphytic bryophytes at higher altitudinal plots
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13 in our study. Thus, future predicted changes in climate may alter the suitability of these
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15 conditions for climate-sensitive epiphytes in Honduras, both directly by changes in climate and
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17 indirectly by likely decreases in moisture availability through the bryophyte branch
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19 communities. Bryophytes, specifically, can be important for the survival of epiphytic ferns, as
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21 increased bryophyte cover facilitates epiphyte establishment (Winkler *et al.* 2005) as well as
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23 water interception and storage (Ah-Peng *et al.* 2017, Oishi 2018). In addition, water
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25 availability is an important aspect in the fern life cycle as well as for the survival of mature
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27 plants, which have less specific stomatal control than angiosperms (McAdam & Brodribb
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29 2013).

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35 Comparisons with previous studies of altitudinal distribution patterns in relation to climate
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37 change are challenging, due to the complete lack of studies within Honduras and limited studies
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39 that investigated tropical epiphytic ferns and lycophytes. Interestingly, we found that epiphyte
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41 richness was particularly high at high elevation sites, which we believed was one of the key
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43 driving factors for epiphytes exhibiting a higher range loss compared to terrestrial species under
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45 future predicted changes in climate. In comparison, other studies that investigated vascular
46
47 epiphyte richness along mountains, often found a mid-elevation peak in species richness (Hsu
48
49 *et al.* 2014, Pouteau *et al.* 2016). Therefore, it is likely that the underlying distribution patterns
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51 of ferns and lycophytes at a given site will ultimately determine the severity of climate change
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53 on the specific life-form ranges (e.g. epiphytes versus terrestrial species).
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3 In conclusion, higher temperatures under future predicted climate change may contribute to
4 increases in total canopy evapotranspiration (Calanca *et al.* 2006, Jung *et al.* 2010), particularly
5 at higher altitudinal sites. With climate change forecasts predicting rising global temperatures
6 and decreases in precipitation (IPCC 2014), tropical montane forests are likely to experience
7 reductions in cloud immersion due to a shift in cloud layers (Foster 2001, Karmalkar *et al.*
8 2011, Lawton *et al.* 2001, Still *et al.* 1999). These indirect effects of changing climatic
9 conditions have the potential to exacerbate epiphyte species up-wards range shifts in the
10 tropical montane forests of Honduras (Nadkarni & Solano 2002), as demonstrated in our study.
11 To minimise the potential negative effect of these up-wards range shifts under future changes
12 in climate, at least at a local and regional level, current conservation strategies in Honduras
13 would require drastic conservation interventions (e.g. assistant migration and ex-situ
14 conservation methods) in order to ensure the survival of many of these high-altitude species.
15 However, a lack of robust information on the distribution of ferns across most of Honduras
16 exacerbates the problem. This issue must be addressed as climate change induced species
17 responses will ultimately affect plant community composition and distributions in Honduras
18 and elsewhere. The highest mountain in Honduras studied here, has and will in the future,
19 provide insight for the first time into how quickly plant communities will respond to changes
20 in climate. Our study has already indicated that specifically high-altitude fern communities in
21 Celaque will change and/or disappear, and it is likely that similar responses threaten species
22 elsewhere.
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References

- ACEVEDO, M. A., BEAUDROT, L., MELÉNDEZ-ACKERMAN, E. J. & TREMBLAY, R. L. 2020. Local extinction risk under climate change in a neotropical asymmetrically dispersed epiphyte. *Journal of Ecology* 108(4):1553-1564.
- ADAMS, H. D. & KOLB, T. E. 2005. Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *Journal of Biogeography* 32(9):1629-1640.
- AH-PENG, C., CARDOSO, A. W., FLORES, O., WEST, A., WILDING, N., STRASBERG, D. & HEDDERSON, T. A. J. 2017. The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *Journal of Hydrology* 548:665-673.
- ALLEN, J. L. & LENDEMER, J. C. 2016. Climate change impacts on endemic, high-elevation lichens in a biodiversity hotspot. *Biodiversity and Conservation* 25(3):555-568.
- ANDERSON, R. S. & ASHE, J. S. 2000. Leaf litter inhabiting beetles as surrogates for establishing priorities for conservation of selected tropical montane cloud forests in Honduras, Central America (Coleoptera; Staphylinidae, Curculionidae). *Biodiversity & Conservation* 9(5):617-653.
- ARCHAGA, V. 1998. Descripción física y caracterización del Parque Nacional Montaña de Celaque. Pp. 15. AFE-COHDEFOR y GTZ, Santa Rosa de Copán. 15 pp.
- BATKE, S., CASCANTE-MARÍN, A. & KELLY, D. L. 2016. Epiphytes in Honduras: a geographical analysis of the vascular epiphyte flora and its floristic affinities to other Central American countries. *Tropical Ecology* 57(4).
- BATKE, S. P. & 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(5):457-467.
- BATKE, S. P. & KELLY, D. L. 2015. Changes in the distribution of mechanically dependent plants along a gradient of past hurricane impact. *AoB Plants*.
- BENZING, D. H. 1990. Vascular epiphytes - general biology and related biota. Cambridge University Press, Cambridge. 376 pp.

- 1
2
3 BENZING, D. H. 1998. Vulnerabilities of tropical forests to climate change: the significance
4 of resident epiphytes. *Climatic Change* 39(2):519-540.
- 5 BHATTARAI, K. R., VETAAS, O. R. & GRYTNES, J. A. 2004. Fern species richness along
6 a central Himalayan elevational gradient, Nepal. *Journal of Biogeography* 31(3):389-400.
- 7 BRESHEARS, D. D., HUXMAN, T. E., ADAMS, H. D., ZOU, C. B. & DAVISON, J. E.
8 2008. Vegetation synchronously leans upslope as climate warms. *Proceedings of the National
9 Academy of Sciences* 105(33):11591-11592.
- 10 BRUCE, P., BRUCE, A. & GEDECK, P. 2020. Practical statistics for data scientists: 50+
11 essential concepts using R and Python. O'Reilly Media.
- 12 BURT, T. & HOLDEN, J. 2010. Changing temperature and rainfall gradients in the British
13 Uplands. *Climate Research* 45:57-70.
- 14 CALANCA, P., ROESCH, A., JASPER, K. & WILD, M. 2006. Global warming and the
15 summertime evapotranspiration regime of the alpine region. *Climatic Change* 79(1):65-78.
- 16 CALCAGNO, V. & DE MAZANCOURT, C. 2010. glmulti: an R package for easy
17 automated model selection with (generalized) linear models. *Journal of statistical software*
18 34(12):1-29.
- 19 CARDELUS, C. L., COLWELL, R. K. & WATKINS, J. E. 2006. Vascular epiphyte
20 distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology*
21 94(1):144-156.
- 22 CHÁVEZ, J. D. R., MARADIAGA, R. F. D. & RODRÍGUEZ, H. L. V. 2020. New records
23 and notes on the genus *Phanerophlebia* (Dryopteridaceae) in Honduras. *Acta Botanica
24 Mexicana* (127).
- 25 COLWELL, R. K., BREHM, G., CARDELÚS, C. L., GILMAN, A. C. & LONGINO, J. T.
26 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics.
27 *Science* 322(5899):258-261.
- 28 DI NUZZO, L., VALLESE, C., BENESPERI, R., GIORDANI, P., CHIARUCCI, A., DI
29 CECCO, V., DI MARTINO, L., DI MUSCIANO, M., GHEZA, G. & LELLI, C. 2021.
30 Contrasting multitaxon responses to climate change in Mediterranean mountains. *Scientific
31 reports* 11(1):1-12.
- 32 ELLIS, C. J. 2013. A risk-based model of climate change threat: hazard, exposure, and
33 vulnerability in the ecology of lichen epiphytes. *Botany* 91(1):1-11.
- 34 ELLIS, C. J. & COPPINS, B. J. 2007. Changing climate and historic-woodland structure
35 interact to control species diversity of the 'Lobarion' epiphyte community in Scotland.
36 *Journal of Vegetation Science* 18(5):725-734.
- 37 ELLIS, C. J. & COPPINS, B. J. 2009. Quantifying the role of multiple landscape-scale
38 drivers controlling epiphyte composition and richness in a conservation priority habitat
39 (juniper scrub). *Biological Conservation* 142(7):1291-1301.
- 40 ELLIS, C. J. & COPPINS, B. J. 2010. Integrating multiple landscape-scale drivers in the
41 lichen epiphyte response: climatic setting, pollution regime and woodland spatial-temporal
42 structure. *Diversity and Distributions* 16(1):43-52.
- 43 ESRI. 2020. ArcGIS. ESRI (Environmental Systems Resource Institute), Redlands,
44 California.
- 45 EVANS, A. M. 1964. Ameiotic alternation of generations: a new life cycle in the ferns.
46 *Science* 143(3603):261-263.
- 47 FEELEY, K. J. & SILMAN, M. R. 2010. Biotic attrition from tropical forests correcting for
48 truncated temperature niches. *Global Change Biology* 16(6):1830-1836.
- 49 FLORES, E., SÁNCHEZ, A., CASTELLANOS, N., ÁVILA, R., ZELAYA, E. & PAZ, G.
50 2012. Plan de Manejo Parque Nacional Montaña de Celaque periodo 2012-2016. Pp. 173.
51 Mancomunidad de Municipios del Parque Nacional Montaña de Celaque (MAPANCE),
52
53
54
55
56
57
58
59
60

- Instituto de Conservación Forestal (ICF), Deutsche Gesellschaft Fur Internationale Zusammenarbeit (GIZ). 173 pp.
- FOSTER, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* 55(1-2):73-106.
- FRAHM, J.-P. & GRADSTEIN, S. R. 1991. An altitudinal zonation of tropical rain forests using bryophytes. *Journal of Biogeography* 18(6):669-678.
- FREEMAN, B. G., LEE-YAW, J. A., SUNDAY, J. M. & HARGREAVES, A. L. 2018. Expanding, shifting and shrinking: The impact of global warming on species' elevational distributions. *Global Ecology and Biogeography* 27(11):1268-1276.
- GIBSON-REINEMER, D. K. & RAHEL, F. J. 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. *PLoS ONE* 10(7):e0132103.
- GONZALES, J. & KESSLER, M. 2011. A synopsis of the Neotropical species of *Sticherus* (Gleicheniaceae), with descriptions of nine new species. *Phytotaxa* 31(1):1-54.
- GRAU, O., GRYTNES, J.-A. & BIRKS, H. J. B. 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography* 34(11):1907-1915.
- GRAU, O., NINOT, J., FONT, X., FERRÉ, A. & GRYTNES, J.-A. 2011. Trends in altitudinal distribution of plant diversity in the Catalan Pyrenees. Pp. 171-180. *Actes del IX col·loqui Internacional de Botànica Pirenaico-cantàbrica A ordIno*. Andorra. 171-180 pp.
- HASSLER, M. & SCHMITT, B. 2020. Checklist of Ferns and Lycophytes of the World. Botanical Garden of the Karlsruhe Institute of Technology, <https://worldplants.webarchiv.kit.edu/ferns/statistics.php>.
- HERMES, V., CETZAL-IX, W., EDGAR, M. & ROMERO-SOLER, K. 2016. Nuevos registros para la flora de Honduras y el Parque Nacional Montaña de Celaque. *Acta Biologica Colombiana* 21(3):635-644.
- HIETZ, P. & HIETZ-SEIFERT, U. 1995. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science* 6(4):487-498.
- HSU, R. C.-C., OOSTERMEIJER, J. G. B. & WOLF, J. H. 2014. Adaptation of a widespread epiphytic fern to simulated climate change conditions. *Plant ecology* 215(8):889-897.
- HSU, R. C.-C., TAMIS, W. L. M., RAES, N., DE SNOO, G. R., WOLF, J. H. D., OOSTERMEIJER, G. & LIN, S.-H. 2012. Simulating climate change impacts on forests and associated vascular epiphytes in a subtropical island of East Asia. *Diversity and Distributions* 18(4):334-347.
- IBISCH, P. L., BOEGNER, A., NIEDER, J. & BARTHOLOTT, W. 1996. How diverse are neotropical epiphytes? An analysis based on the 'Catalogue of the flowering plants and gymnosperms of Peru'. *Ecotropica* 2:13-28.
- ICF. 2016. Plan de Manejo del Parque Nacional Montaña de Celaque 2016-2027. Pp. 87.
- ICF, MAPANCE, Gracias, Lempiras. 87 pp.
- IMBACH, P. A., LOCATELLI, B., MOLINA, L. G., CIAIS, P. & LEADLEY, P. W. 2013. Climate change and plant dispersal along corridors in fragmented landscapes of Mesoamerica. *Ecology and Evolution* 3(9):2917-2932.
- IPCC. 2014. Climate Change 2014: impacts, adaptation, and vulnerability. Fifth assessment report of the Intergovernmental Panel on Climate Change Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA. 1132 pp.
- IPCC. 2018. Summary for Policymakers. in Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P. R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S., Matthews, J. B. R., Chen, Y., Zhou, X., Gomis, M. I., Lonnoy, E., Maycock, T., Tignor, M. & Waterfield, T. (eds.). Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global

- greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. IPCC, In press.
- JANSSEN, P., FUHR, M. & BOUGET, C. 2019. Beyond forest habitat qualities: Climate and tree characteristics as the major drivers of epiphytic macrolichen assemblages in temperate mountains. *Journal of Vegetation Science* 30(1):42-54.
- JONES, S. E., TOBIAS, J. A., FREEMAN, R. & PORTUGAL, S. J. 2020. Weak asymmetric interspecific aggression and divergent habitat preferences at an elevational contact zone between tropical songbirds. *Ibis* 162(3):814-826.
- JUMP, A. S., HUANG, T.-J. & CHOU, C.-H. 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. *Ecography* 35(3):204-210.
- JUNG, M., REICHSTEIN, M., CIAIS, P., SENEVIRATNE, S. I., SHEFFIELD, J., GOULDEN, M. L., BONAN, G., CESCATTI, A., CHEN, J., DE JEU, R., DOLMAN, A. J., EUGSTER, W., GERTEN, D., GIANELLE, D., GOBRON, N., HEINKE, J., KIMBALL, J., LAW, B. E., MONTAGNANI, L., MU, Q., MUELLER, B., OLESON, K., PAPALE, D., RICHARDSON, A. D., ROUPSARD, O., RUNNING, S., TOMELLERI, E., VIOVY, N., WEBER, U., WILLIAMS, C., WOOD, E., ZAEHLE, S. & ZHANG, K. 2010. Recent decline in the global land evapotranspiration trend due to limited moisture supply. *Nature* 467(7318):951-954.
- KARGER, D. N., CONRAD, O., BÖHNER, J., KAWOHL, T., KREFT, H., SORIA-AUZA, R. W., ZIMMERMANN, N. E., LINDER, H. P. & KESSLER, M. 2017. Climatologies at high resolution for the earth's land surface areas. *Scientific Data* 4(1):170122.
- KARGER, D. N., KLUGE, J., ABRAHAMCZYK, S., SALAZAR, L., HOMEIER, J., LEHNERT, M., AMOROSO, V. B. & KESSLER, M. 2012. Bryophyte cover on trees as proxy for air humidity in the tropics. *Ecological Indicators* 20(0):277-281.
- KARGER, D. N., WEIGELT, P., AMOROSO, V. B., DARNAEDI, D., HIDAYAT, A., KREFT, H. & KESSLER, M. 2014. Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago. *Journal of Biogeography* 41(2):250-260.
- KARMALKAR, A. V., BRADLEY, R. S. & DIAZ, H. F. 2011. Climate change in Central America and Mexico: regional climate model validation and climate change projections. *Climate Dynamics* 37(3):605.
- KESSLER, M. 2001. Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation* 10(11):1897-1921.
- KESSLER, M. & BACH, K. 1999. Using indicator families for vegetation classification in species-rich Neotropical forests. *Phytocoenologia* 29(4):485-502.
- KESSLER, M., HERZOG, S. K., FJELDSÅ, J. & BACH, K. 2001. Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and Distributions* 7(1-2):61-77.
- KESSLER, M., KARGER, D. N. & KLUGE, J. 2016. Elevational diversity patterns as an example for evolutionary and ecological dynamics in ferns and lycophytes. *Journal of Systematics and Evolution* 54(6):617-625.
- KIDANE, Y. O., STEINBAUER, M. J. & BEIERKUHNLIN, C. 2019. Dead end for endemic plant species? A biodiversity hotspot under pressure. *Global Ecology and Conservation* 19:e00670.
- KLUGE, J. & KESSLER, M. 2011. Influence of niche characteristics and forest type on fern species richness, abundance and plant size along an elevational gradient in Costa Rica. *Plant Ecology* 212(7):1109-1121.

- 1
2
3 KRÖMER, T., KESSLER, M., ROBERT GRADSTEIN, S. & ACEBEY, A. 2005.
4 Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal*
5 *of Biogeography* 32(10):1799-1809.
6 LAWTON, R. O., NAIR, U. S., PIELKE, R. A., SR. & WELCH, R. M. 2001. Climatic
7 impact of tropical lowland deforestation on nearby montane cloud forests. *Science*
8 294(5542):584-587.
9 LENOIR, J., GÉGOUT, J. C., MARQUET, P. A., DE RUFFRAY, P. & BRISSE, H. 2008. A
10 significant upward shift in plant species optimum elevation during the 20th century. *Science*
11 320(5884):1768-1771.
12 LOMOLINO, M. V. 2001. Elevation gradients of species-density: historical and prospective
13 views. *Global Ecology and Biogeography* 10(1):3-13.
14 MANDL, N., LEHNERT, M., KESSLER, M. & GRADSTEIN, S. 2010. A comparison of
15 alpha and beta diversity patterns of ferns, bryophytes and macrolichens in tropical montane
16 forests of southern Ecuador. *Biodiversity and Conservation* 19(8):2359-2369.
17 MARCHESE, C. 2015. Biodiversity hotspots: A shortcut for a more complicated concept.
18 *Global Ecology and Conservation* 3:297-309.
19 MCADAM, S. A. M. & BRODRIBB, T. J. 2012. Stomatal innovation and the rise of seed
20 plants. *Ecology Letters* 15(1):1-8.
21 MCADAM, S. A. M. & BRODRIBB, T. J. 2013. Ancestral stomatal control results in a
22 canalization of fern and lycophyte adaptation to drought. *New Phytologist* 198(2):429-441.
23 MICKEL, J. T. & SMITH, A. R. 2004. The Pteridophytes of Mexico. New York Botanical
24 Garden Press, USA. 727 pp.
25 MORAN, R. 1997. Flora Mesoamericana - Pteridophyta. New York Botanical Garden, USA.
26 MORUETA-HOLME, N., ENGEMANN, K., SANDOVAL-ACUÑA, P., JONAS, J. D.,
27 SEGNITZ, R. M. & SVENNING, J.-C. 2015. Strong upslope shifts in Chimborazo's
28 vegetation over two centuries since Humboldt. *Proceedings of the National Academy of*
29 *Sciences* 112(41):12741-12745.
30 MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B. &
31 KENT, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403(6772):853-858.
32 NADKARNI, N. & SOLANO, R. 2002. Potential effects of climate change on canopy
33 communities in a tropical cloud forest: an experimental approach. *Oecologia* 131(4):580-586.
34 NEATE-CLEGG, M. H., JONES, S. E., BURDEKIN, O., JOCQUE, M. & ŞEKERCIOĞLU,
35 Ç. H. 2018. Elevational changes in the avian community of a Mesoamerican cloud forest
36 park. *Biotropica* 50(5):805-815.
37 NERVO, M. H., ANDRADE, B. O., TORNQUIST, C. G., MAZURANA, M., WINDISCH,
38 P. G. & OVERBECK, G. E. 2019. Distinct responses of terrestrial and epiphytic ferns and
39 lycophytes along an elevational gradient in Southern Brazil. *Journal of Vegetation Science*
40 30(1):55-64.
41 OISHI, Y. 2018. Evaluation of the water-storage capacity of bryophytes along an altitudinal
42 gradient from temperate forests to the alpine zone. *Forests* 9(7):433.
43 POUTEAU, R., MEYER, J.-Y., BLANCHARD, P., NITTA, J. H., TEROROTUA, M. &
44 TAPUTUARAI, R. 2016. Fern species richness and abundance are indicators of climate
45 change on high-elevation islands: evidence from an elevational gradient on Tahiti (French
46 Polynesia). *Climatic Change* 138(1):143-156.
47 PPGI. 2016. A community-derived classification for extant lycophytes and ferns. *Journal of*
48 *Systematics and Evolution* 54(6):563-603.
49 PROCTOR, M. C. F. 2003. Comparative ecophysiological measurements on the light
50 responses, water relations and desiccation tolerance of the filmy ferns *Hymenophyllum*
51 *wilsonii* Hook. and *H. tunbrigense* (L.) Smith. *Annals of Botany* 91(6):717-727.
52
53
54
55
56
57
58
59
60

- 1
2
3 R DEVELOPING CORE TEAM. 2020. R: a language and environment for statistical
4 computing R Foundation for Statistical Computing, R Foundation for Statistical Computing,
5 Vienna, Austria. URL <http://www.R-project.org/>.
6
7 RAHBEK, C. 1995. The elevational gradient of species richness: a uniform pattern?
8 *Ecography* 18(2):200-205.
9 REYES-CHÁVEZ, J., FABIOLA, R. & VEGA, H. 2018. Actualización taxonómica de las
10 pteridofitas y licófitas (helechos) del Parque Nacional Montaña de Celaque, Honduras.
11 *Revista Rosalia* 1(5):26-35.
12 RICHARDS, P. & EVANS, G. 1972. Biological flora of the British Isles: *Hymenophyllum*.
13 *Journal of Ecology*.
14 RICHARDS, P. W. 1952. The Tropical Rain Forest: An Ecological Study (2 edition).
15 Cambridge University Press.
16 ROGORA, M., FRATE, L., CARRANZA, M. L., FREPPAZ, M., STANISCI, A.,
17 BERTANI, I., BOTTARIN, R., BRAMBILLA, A., CANULLO, R., CARBOGNANI, M.,
18 CERRATO, C., CHELLI, S., CREMONESE, E., CUTINI, M., DI MUSCIANO, M.,
19 ERSCHBAMER, B., GODONE, D., IOCCHI, M., ISABELLON, M., MAGNANI, A.,
20 MAZZOLA, L., MORRA DI CELLA, U., PAULI, H., PETEY, M., PETRICCIONE, B.,
21 PORRO, F., PSENNER, R., ROSSETTI, G., SCOTTI, A., SOMMARUGA, R.,
22 TAPPEINER, U., THEURILLAT, J. P., TOMASELLI, M., VIGLIETTI, D., VITERBI, R.,
23 VITTOZ, P., WINKLER, M. & MATTEUCCI, G. 2018. Assessment of climate change
24 effects on mountain ecosystems through a cross-site analysis in the Alps and Apennines.
25 *Science of the Total Environment* 624:1429-1442.
26
27 ROJAS-ALVARADO, A. F. 2003. New taxa, new records and redefined concepts in the
28 *Elaphoglossum* sect. *Elaphoglossum* subsec. *Pachyglossa* (Lomariopsidaceae) from Mexico
29 and Central America. *Revista de Biología Tropical* 51(1):1-32.
30
31 ROJAS-ALVARADO, A. F. 2012. Nuevos registros de licopodios (Lycopodiophyta) y
32 helechos (Pteridophyta) para Honduras y el Parque Nacional Montañas de Celaque. *Revista*
33 *Biodiversidad Neotropical* 2(2):83-92.
34
35 ROJAS-ALVARADO, A. F. 2017. Three new species of ferns (Pteridophyta) from
36 Mesoamerica. *American Journal of Plant Sciences* 8(6):1329-1338.
37
38 SAIZ, H., DAINESE, M., CHIARUCCI, A. & NASCIMBENE, J. 2021. Networks of
39 epiphytic lichens and host trees along elevation gradients: Climate change implications in
40 mountain ranges. *Journal of Ecology* 109(3):1122-1132.
41
42 SÁNCHEZ-GONZÁLEZ, A., ZÚÑIGA, E. Á. & TEJERO-DÍEZ, J. D. 2010. Richness and
43 distribution patterns of ferns and lycopods in Los Mármoles National Park, Hidalgo, Mexico.
44 *The Journal of the Torrey Botanical Society* 137(4):373-379.
45
46 SMITH, P., PRICE, J., MOLOTOKS, A., WARREN, R. & MALHI, Y. 2018. Impacts on
47 terrestrial biodiversity of moving from a 2 C to a 1.5 C target. *Philosophical Transactions of*
48 *the Royal Society A: Mathematical, Physical and Engineering Sciences* 376(2119):20160456.
49
50 SONG, L., LIU, W.-Y. & NADKARNI, N. M. 2012. Response of non-vascular epiphytes to
51 simulated climate change in a montane moist evergreen broad-leaved forest in southwest
52 China. *Biological Conservation* 152:127-135.
53
54 SOUTHWORTH, J., NAGENDRA, H., CARLSON, L. A. & TUCKER, C. 2004. Assessing
55 the impact of Celaque National Park on forest fragmentation in western Honduras. *Applied*
56 *Geography* 24(4):303-322.
57
58 STILL, C. J., FOSTER, P. N. & SCHNEIDER, S. H. 1999. Simulating the effects of climate
59 change on tropical montane cloud forests. *Nature* 398(6728):608-610.
60
61 STROUD, J. T. & FEELEY, K. J. 2017. Neglect of the tropics is widespread in ecology and
62 evolution: A comment on Clarke et al. *Trends in ecology & evolution* 32(9):626-628.

- 1
2
3 WARREN, R., PRICE, J., GRAHAM, E., FORSTENHAEUSLER, N. & VANDERWAL, J.
4 2018. The projected effect on insects, vertebrates, and plants of limiting global warming to
5 1.5 C rather than 2 C. *Science* 360(6390):791-795.
- 6 WATKINS, J. E., CATHERINE, C., COLWELL, R. K. & MORAN, R. C. 2006. Species
7 richness and distribution of ferns along an elevational gradient in Costa Rica. *American*
8 *Journal of Botany* 93(1):73-83.
- 9 WINKLER, M., HÜLBER, K. & HIETZ, P. 2005. Effect of canopy position on germination
10 and seedling survival of epiphytic bromeliads in a Mexican humid montane forest. *Annals of*
11 *Botany* 95(6):1039-1047.
- 12 WOLF, A., ZIMMERMAN, N. B., ANDEREGG, W. R. L., BUSBY, P. E. &
13 CHRISTENSEN, J. 2016. Altitudinal shifts of the native and introduced flora of California in
14 the context of 20th-century warming. *Global Ecology and Biogeography* 25(4):418-429.
- 15 WOLF, J. H. D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens
16 along an altitudinal gradient in the Northern Andes. *Annals of the Missouri Botanical Garden*
17 80(4):928-960.
- 18 ZHOU, Y., OCHOLA, A. C., NJOGU, A. W., BORU, B. H., MWACHALA, G., HU, G.,
19 XIN, H. & WANG, Q. 2019. The species richness pattern of vascular plants along a tropical
20 elevational gradient and the test of elevational Rapoport's rule depend on different life-forms
21 and phytogeographic affinities. *Ecology and Evolution* 9(8):4495-4503.
- 22 ZOTZ, G. & BADER, M. 2009. Epiphytic plants in a changing world-global: change effects
23 on vascular and non-vascular epiphytes. Pp. 147-170. *Progress in Botany*. Springer.
- 24 ZOTZ, G. & HIETZ, P. 2001. The physiological ecology of vascular epiphytes: current
25 knowledge, open questions. *Journal of Experimental Botany* 52(364):2067-2078.
- 26 ZOTZ, G., HIETZ, P. & SCHMIDT, G. 2001. Small plants, large plants: the importance of
27 plant size for the physiological ecology of vascular epiphytes. *Journal of Experimental*
28 *Botany* 52(363):2051-2056.
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Table 1. Random/mixed-effects meta-regression model results for the best fit models, where NMS axis 1 and 2 and Simpson diversity was modelled as a response variable for different explanatory variables. AIC was used to select the best fit model for each response variable.

Response variable	Explanatory variables	Estimate	Std. Error	t-value	p-value
Axis 1 (AIC=8.69)	Altitude	0.0017	0.0001	16.18	<0.01
	Bryophyte cover	0.0069	0.0017	3.95	<0.01
	Percentage cover (-10)	-0.0021	0.0018	-1.16	ns
	Precipitation	0.0014	0.0006	2.24	<0.05
Axis 2 (AIC=115.86)	Bryophyte cover	-0.0081	0.0029	-2.80	<0.01
	Rock cover	-0.0060	0.0031	-1.96	ns
	Percentage cover (-10)	-0.0052	0.0034	-1.52	ns
	Precipitation	-0.0023	0.0010	-2.33	<0.05
Simpson epiphytes (AIC=117.22)	Bryophyte cover	0.0157	0.0035	4.46	<0.01
	Percentage cover (-10)	-0.0064	0.0037	-1.74	ns
	Temperature	-0.0753	0.0311	-2.42	<0.05

Simpson
terrestrial

Bryophyte cover

(AIC=111.59)

0.0058	0.0030	1.91	ns	
Canopy height	-0.0105	0.0082	-1.28	ns
Percentage cover	0.0063	0.0038	1.69	ns
Inclination	0.0076	0.0047	1.63	ns
Precipitation	0.0034	0.0010	3.52	<0.01

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18 **Table 2.** Number of species per life-forms for each year and climate change scenario that are
 19 likely to loss part or all of their range.

Range					
lost	Life-form	2050		2100	
		RCP2.6	RCP8.5	RCP2.6	RCP8.5
None	Epiphyte	37	37	29	23
	Terrestrial	60	61	54	40
	Sub-total	97	98	83	63
Some	Epiphyte	37	37	31	35
	Terrestrial	19	18	19	31
	Sub-total	56	55	50	66
All	Epiphyte	4	4	18	20
	Terrestrial	3	3	9	11
	Sub-total	7	7	27	31
Total		160	160	160	160

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3 27 **Figure 1.** Digital elevation model (DEM) of Celaque National Park. Points show the sample
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5 28 locations (n=80).
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11 30 **Figure 2.** Plot species richness along an altitudinal gradient in Celaque National Park,
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14 31 Honduras (A). Spline regression was fitted with a series of polynomial segments. The mean
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16 32 (solid lines) and standard error (grey shading) are shown only for visualisation purposes.
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18 33 Multidimensional scaling of the community composition data (all life-forms) was used to
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20 34 identify community similarities between altitudinal plots (n=80) (B). Panel B shows a 2-
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23 35 dimensional ordination of axis 1 and 2 with individual plots highlighted by different colours
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25 36 based on their altitude (blue to red = low to high altitude).
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32 38 **Figure 3.** Relative model-averaged importance of terms calculated using a random/mixed-
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34 39 effects meta-regression model for NMS axis 1 (A), axis 2 (B) and Simpson epiphyte (C) and
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36 40 terrestrial diversity (D). The importance for a predictor is equal to the sum of the weights for
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38 41 the models in which the variable appears. The vertical red line is drawn at 0.8 and denotes the
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40 42 cutoff to differentiate between important and less important variables. The model results that
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42 43 are shown for each of the first three variable terms, are the best-fit models following AIC
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44 44 selection. The plus and minus symbols denote the direction of the relationships.
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4 48 **Figure 4.** Mean annual temperature (A) and precipitation (B) for the 80 sample locations at
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6 49 Celaque National Park, Honduras. Current mean annual temperature and precipitation was
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8 50 extracted from Karger *et al.* (2017). Climate projections of western Honduras for the years
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10 51 2050 and 2100 were extracted from IPCC (2014). Current = blue dots; RCP2.6 for 2050 =
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12 52 green triangles; RCP2.6 for 2100 = yellow squares; RCP8.5 for 2050 = orange pluses; RCP2.6
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14 53 for 2050 = grey squares with a diagonal cross.

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21 55 **Figure 5.** Current and projected species altitudinal ranges for RCP2.4 and 8.5 for the year 2050
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23 56 and 2100, separated between epiphytic (A) and terrestrial species (B). Each horizontal line
24
25 57 represents a single species. For visualization purposes, the species names are not shown on the
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27 58 y-axis for panel A and B. The vertical dashed line shows the maximum altitude of the mountain.
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29 59 Panel (C) shows the density distribution of the percentage altitudinal range lost for each
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31 60 scenario and year, weighted by the number of species. Current = blue; RCP2.6 for 2050 =
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33 61 green; RCP2.6 for 2100 = yellow; RCP8.5 for 2050 = orange; RCP2.6 for 2050 = grey.

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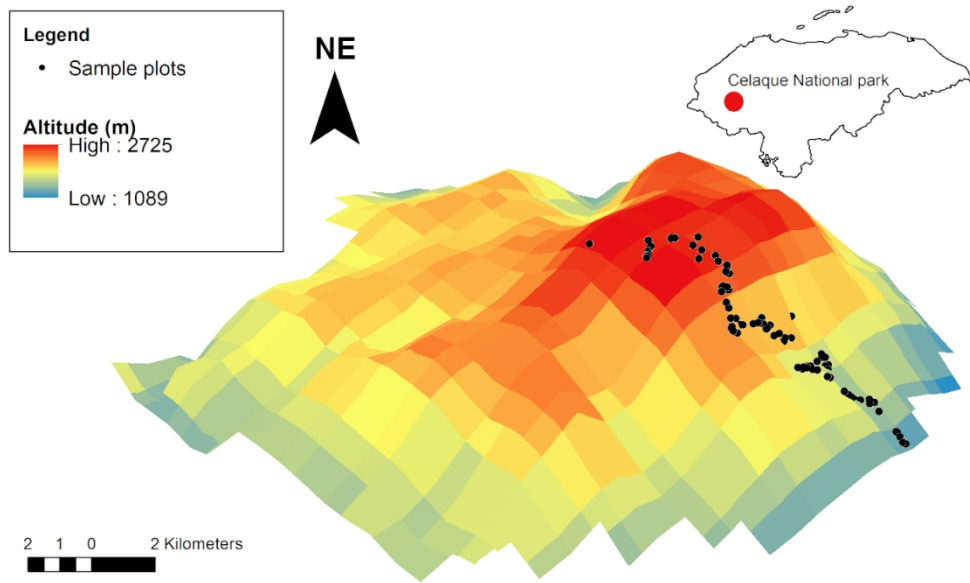


Figure 1. Digital elevation model (DEM) of Celaque National Park. Points show the sample locations (n=80).

112x70mm (300 x 300 DPI)

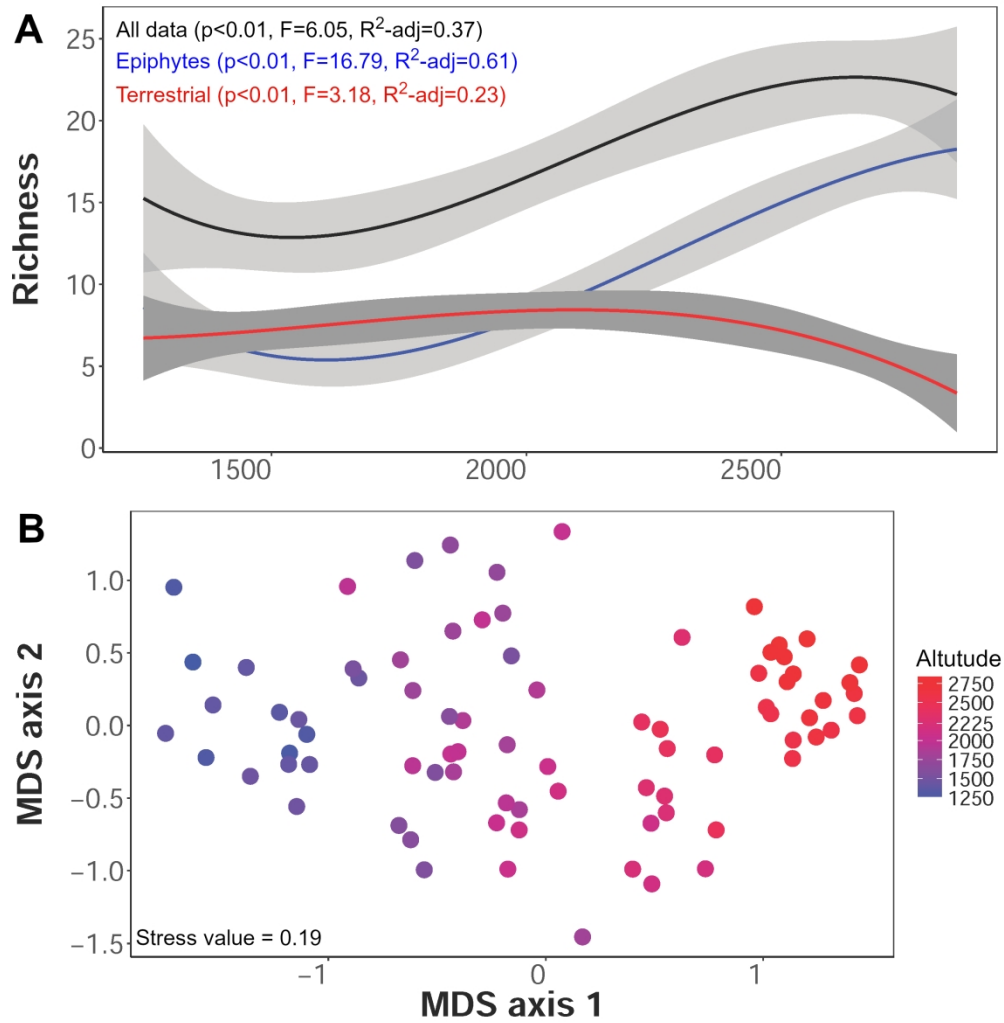


Figure 2. Plot species richness along an altitudinal gradient in Celaque National Park, Honduras (A). Spine regression was fitted with a series of polynomial segments. The mean (solid lines) and standard error (grey shading) are shown only for visualisation purposes. Multidimensional scaling of the community composition data (all life-forms) was used to identify community similarities between altitudinal plots ($n=80$) (B). Panel B shows a 2-dimensional ordination of axis 1 and 2 with individual plots highlighted by different colours based on their altitude (blue to red = low to high altitude).

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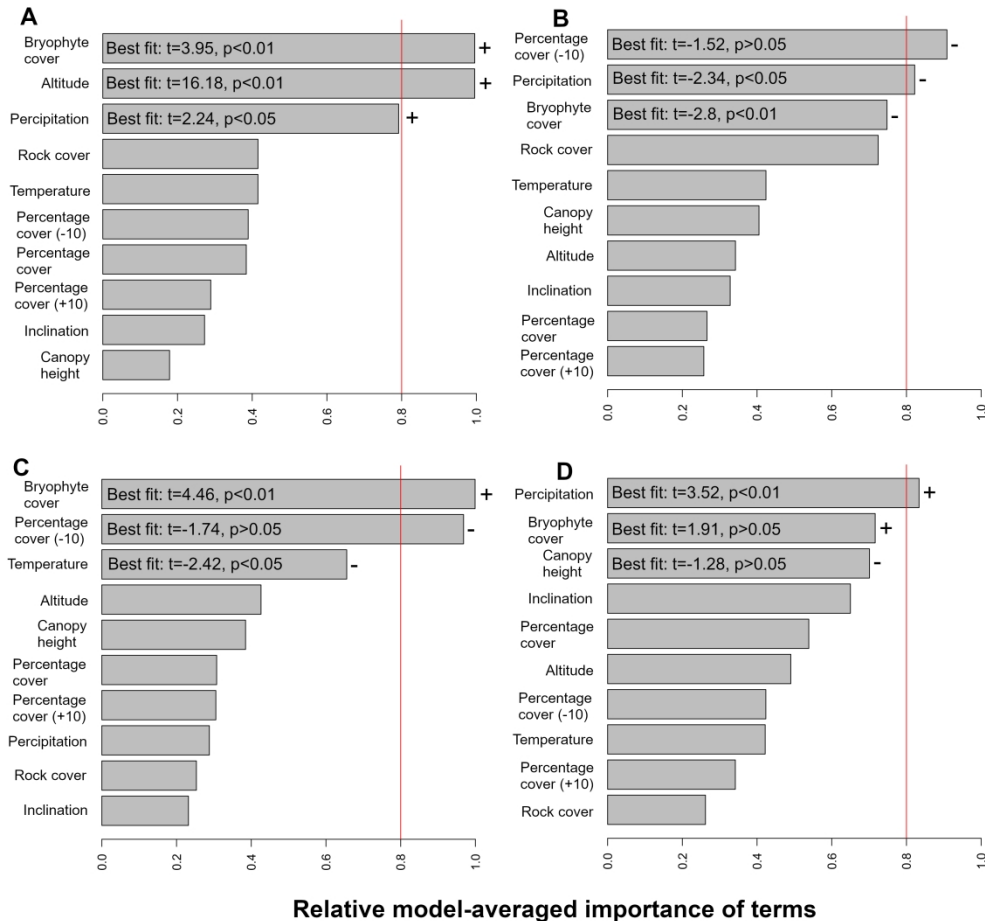


Figure 3. Relative model-averaged importance of terms calculated using a random/mixed-effects meta-regression model for NMS axis 1 (A), axis 2 (B) and Simpson epiphyte (C) and terrestrial diversity (D). The importance for a predictor is equal to the sum of the weights for the models in which the variable appears.

The vertical red line is drawn at 0.8 and denotes the cutoff to differentiate between important and less important variables. The model results that are shown for each of the first three variable terms, are the best-fit models following AIC selection. The plus and minus symbols denote the direction of the relationships.

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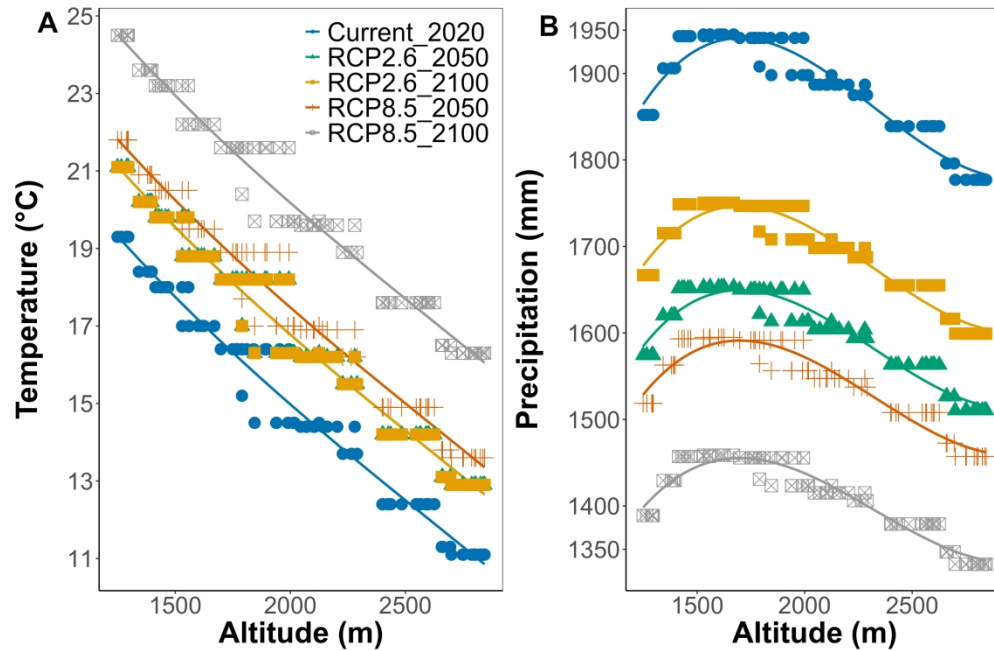


Figure 4. Mean annual temperature (A) and precipitation (B) for the 80 sample locations at Celaque National Park, Honduras. Current mean annual temperature and precipitation was extracted from Karger et al. (2017). Climate projections of western Honduras for the years 2050 and 2100 were extracted from IPCC (2014). Current = blue dots; RCP2.6 for 2050 = green triangles; RCP2.6 for 2100 = yellow squares; RCP8.5 for 2050 = orange pluses; RCP2.6 for 2050 = grey squares with a diagonal cross.

296x194mm (300 x 300 DPI)

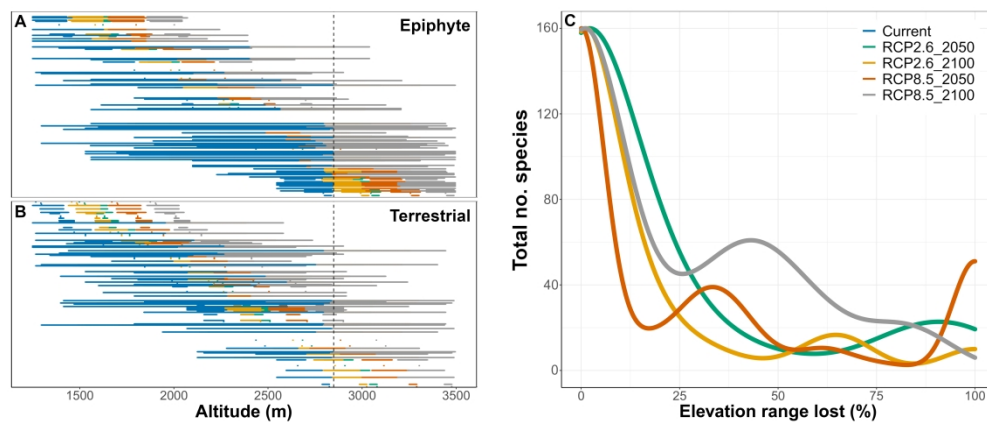


Figure 5. Current and projected species altitudinal ranges for RCP2.4 and 8.5 for the year 2050 and 2100, separated between epiphytic (A) and terrestrial species (B). Each horizontal line represents a single species. For visualization purposes, the species names are not shown on the y-axis for panel A and B. The vertical dashed line shows the maximum altitude of the mountain. Panel (C) shows the density distribution of the percentage altitudinal range lost for each scenario and year, weighted by the number of species. Current = blue; RCP2.6 for 2050 = green; RCP2.6 for 2100 = yellow; RCP8.5 for 2050 = orange; RCP2.6 for 2050 = grey.

504x209mm (300 x 300 DPI)

Supplementary material

Supplementary Table 1. Species list of ferns and lycophytes from Celaque National Park. Columns summarize the percentage of range lost for each species based on IPCC predictions for the year 2050 and 2100 (RCP2.6 and 8.5 scenarios).

Species	2050		2100	
	RCP2.6	RCP8.5	RCP2.6	RCP8.5
<i>Adiantum andicola</i> Liebm.	0	0	10	31
<i>Adiantum concinnum</i> Humb. & Bonpl. ex Willd.	0	0	0	0
<i>Adiantum feei</i> T. Moore ex Fée	18	13	38	56
<i>Alansmia cultrate</i> (Willd.) Moguel & M. Kessler	0	0	0	0
<i>Amauropelta pilosohispida</i> (Hook.) A.R. Sm.	17	11	41	62
<i>Amauropelta pilosula</i> (Klotzsch & H. Karst. ex Mett.) Á. Löve & D. Löve	0	0	0	0
<i>Amauropelta resinifera</i> (Desv.) Pic. Serm.	19	15	34	49
<i>Anemia karwinskyana</i> (C. Presl) Prantl	19	15	34	48
<i>Anemia phyllitidis</i> (L.) Sw.	0	0	0	0
<i>Arachniodes denticulate</i> (Sw.) Ching	0	0	0	0
<i>Ascogrammitis anfractuosa</i> (Kunze ex Klotzsch) Sundue	0	0	0	0
<i>Asplenium abscissum</i> Willd.	100	100	100	100
<i>Asplenium achilleifolium</i> (M. Martens & Galeotti) Liebm.	100	100	100	100
<i>Asplenium auriculatum</i> (Thunb.) Kuhn	0	0	0	0
<i>Asplenium auritum</i> Sw.	19	15	34	48
<i>Asplenium blepharophorum</i> Bertol.	0	0	0	10
<i>Asplenium fragrans</i> Sw.	100	100	100	100
<i>Asplenium harpeodes</i> Kunze	0	0	0	0
<i>Asplenium miradoreense</i> Liebm.	0	0	0	0
<i>Asplenium monanthes</i> L.	82	65	100	100
<i>Asplenium praemorsum</i> Sw.	0	0	0	0
<i>Asplenium pumilum</i> Sw.	16	12	32	47
<i>Asplenium radicans</i> L.	0	0	0	0
<i>Asplenium serra</i> Langsd. & Fisch.	0	0	0	0
<i>Asplenium sessilifolium</i> Desv.	0	0	100	100

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3	<i>Asplenium uniseriale</i> Raddi	34	26	64	92
4	<i>Asplenium</i> sp. 1	0	0	0	5
5	<i>Austroblechnum lherminieri</i> (Bory) Gasper &				
6	V.A.O. Dittrich	0	0	0	0
7	<i>Austroblechnum stoloniferum</i> (Mett. ex E.				
8	Fourn.) Gasper & V.A.O. Dittrich	0	0	0	0
9	<i>Blechnum appendiculatum</i> Willd.	13	9	26	38
10	<i>Blechnum falciforme</i> (Liebm.) C. Chr.	19	15	34	48
11	<i>Blechnum glandulosum</i> Kaulf. ex Link	82	64	100	100
12	<i>Blechnum occidentale</i> L.	0	0	0	0
13	<i>Blechnum polypodioides</i> Raddi	0	0	0	0
14	<i>Blechnum</i> sp. 1	0	0	0	0
15	<i>Blechnum</i> sp. 2	11	2	46	80
16	<i>Botrypus virginianus</i> (L.) Michx.	0	0	39	77
17	<i>Campyloneurum amphostenon</i> (Kunze ex				
18	Klotzsch) Fée	44	34	80	100
19	<i>Campyloneurum angustifolium</i> (Sw.) Fée	0	0	0	16
20	<i>Campyloneurum tenuipes</i> Maxon	0	0	0	0
21	<i>Campyloneurum xalapense</i> Fée	0	0	16	35
22	<i>Ceradenia oidiophora</i> (Mickel & Beitel) A.R.				
23	Sm.	0	0	0	36
24	<i>Cibotium regale</i> Verschaff. & Lem.	82	65	100	100
25	<i>Cochlidium rostratum</i> (Hook.) Maxon ex C.				
26	Chr.	13	9	26	38
27	<i>Cochlidium serrulatum</i> (Sw.) L.E. Bishop	0	0	0	0
28	<i>Ctenitis equestris</i> (Kunze) Ching	100	100	100	100
29	<i>Ctenitis grisebachii</i> (Baker) Ching	0	0	0	0
30	<i>Ctenitis hemsleyana</i> (Baker) Copel.	0	0	0	0
31	<i>Ctenitis leonii</i> A. Rojas	82	65	100	100
32	<i>Ctenitis melanosticta</i> (Kunze) Copel.	0	0	8	25
33	<i>Ctenitis</i> sp. 1	0	0	14	31
34	<i>Culcita conifolia</i> (Hook.) Maxon	34	27	62	88
35	<i>Cyathea bicrenate</i> Liebm.	16	12	30	43
36	<i>Cyathea</i> sp. 1	0	0	0	0
37	<i>Cyclosorus</i> sp. 1	19	15	34	49
38	<i>Cystopteris fragilis</i> (L.) Bernh.	11	7	24	37
39	<i>Dennstaedtia globulifera</i> (Poir.) Hieron.	0	0	0	0
40	<i>Dicksonia navarrensis</i> Christ	31	24	57	81
41	<i>Didymoglossum reptans</i> (Sw.) C. Presl	56	44	100	100
42	<i>Diplazium cristatum</i> (Desr.) Alston	0	0	0	0
43	<i>Diplazium franconis</i> Liebm.	0	0	18	36
44	<i>Diplazium lindbergii</i> (Mett.) Christ	14	11	29	43
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4	<i>Diplazium</i> sp. 1	0	0	0	0
5	<i>Diplazium werckleanum</i> Christ	0	0	0	0
6	<i>Dryopteris nubigena</i> Maxon & C.V. Morton	0	0	0	48
7	<i>Dryopteris wallichiana</i> var. <i>wallichiana</i>				
8	(Spreng.) Hyl.	0	0	0	0
9	<i>Elaphoglossum guatemalense</i> (Klotzsch) T.				
10	Moore	0	0	0	0
11	<i>Elaphoglossum lanceum</i> Mickel	0	0	0	0
12	<i>Elaphoglossum latifolium</i> (Sw.) J. Sm.	0	0	0	100
13	<i>Elaphoglossum lonchophyllum</i> (Fée) T.				
14	Moore	0	0	0	0
15	<i>Elaphoglossum mexicanum</i> (E. Fourn.) A.				
16	Rojas	0	0	0	8
17	<i>Elaphoglossum muscosum</i> (Sw.) T. Moore	0	0	0	0
18	<i>Elaphoglossum paleaceum</i> (Hook. & Grev.)				
19	Sledge	86	62	100	100
20	<i>Elaphoglossum peltatum</i> (Sw.) Urb.	0	0	0	0
21	<i>Elaphoglossum sartorii</i> (Liebm.) Mickel	0	0	100	100
22	<i>Elaphoglossum setigerum</i> (Sodirol) Diels	15	11	30	44
23	<i>Elaphoglossum</i> sp. 1	0	0	0	16
24	<i>Elaphoglossum</i> sp. 2	94	61	100	100
25	<i>Elaphoglossum</i> sp. 3	0	0	0	0
26	<i>Elaphoglossum</i> sp. 4	0	0	0	2
27	<i>Elaphoglossum squamipes</i> (Hook.) T. Moore	0	0	0	0
28	<i>Elaphoglossum succubus</i> Mickel	9	4	27	44
29	<i>Equisetum myriochaetum</i> Schltld. & Cham.	0	0	22	46
30	<i>Gaga angustifolia</i> (Kunth) Fay W. Li &				
31	Windham	0	0	0	0
32	<i>Goniopteris nicaraguensis</i> (E. Fourn.) Salino				
33	& T.E. Almeida	32	25	59	84
34	<i>Histiopteris incisa</i> (Thunb.) J. Sm.	19	14	39	58
35	<i>Hymenophyllum crassipetiolatum</i> Stolze	0	0	0	9
36	<i>Hymenophyllum crispum</i> Kunth	0	0	0	0
37	<i>Hymenophyllum fucooides</i> (Sw.) Sw.	79	59	100	100
38	<i>Hymenophyllum myriocarpum</i> Hook.	0	0	0	0
39	<i>Hymenophyllum polyanthos</i> (Sw.) Sw.	87	69	100	100
40	<i>Hymenophyllum pulchellum</i> Schltld. & Cham.	100	100	100	100
41	<i>Hymenophyllum tegularis</i> (Desv.) Proctor &				
42	Lourteig	38	18	100	100
43	<i>Hymenophyllum trapezoidale</i> Liebm.	0	0	0	0
44	<i>Jamesonia flexuosa</i> (Kunth) Christenh.	0	0	0	19
45	<i>Lomaridium ensiforme</i> (Liebm.) Gasper &				
46	V.A.O. Dittrich	0	0	4	26
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<i>Lophosoria quadripinnata</i> (J.F. Gmel.) C. Chr.	0	0	0	0
<i>Macrothelypteris torresiana</i> (Gaudich.) Ching	0	0	0	17
<i>Marattia interposita</i> Christ	0	0	0	0
<i>Megalastrum subincisum</i> (Willd.) A.R. Sm. & R.C. Moran	0	0	0	0
<i>Melpomene moniliformis</i> (Lag. ex Sw.) A.R. Sm. & R.C. Moran	66	32	100	100
<i>Melpomene xiphopteroides</i> (Liebm.) A.R. Sm. & R.C. Moran	0	0	0	0
<i>Moranopteris basiattenuata</i> (Jenman) R.Y.Hirai & J.Prado	100	100	100	100
<i>Mycopteris semihirsuta</i> (Klotzsch) Sundue	0	0	0	26
<i>Nephrolepis cordifolia</i> (L.) C. Presl	17	12	32	47
<i>Niphidium crassifolium</i> (L.) Lellinger	16	12	30	43
<i>Osmunda regalis</i> L.	95	69	100	100
<i>Pecluma alfredii</i> (Rosenst.) M.G. Price	0	0	0	0
<i>Pecluma dulcis</i> (Poir.) F.C. Assis & Salino	82	65	100	100
<i>Pecluma hartwegiana</i> (Hook.) F.C. Assis & Salino	99	72	100	100
<i>Phanerophlebia juglandifolia</i> (Humb. & Bonpl. ex Willd.) J. Sm.	0	0	38	77
<i>Phlebodium areolatum</i> (Humb. & Bonpl. ex Willd.) J. Sm.	0	0	0	0
<i>Phlegmariurus myrsinites</i> (Lam.) B. Øllg.	0	0	0	0
<i>Phlegmariurus pringlei</i> (Underw. & F.E. Lloyd) B. Øllg.	0	0	0	13
<i>Phlegmariurus taxifolius</i> (Sw.) Á. Löve & D. Löve	19	12	43	66
<i>Pityrogramma tartarea</i> (Cav.) Maxon	12	5	37	60
<i>Pleopeltis alansmithii</i> (R.C. Moran) A.R. Sm. & Tejero	79	58	100	100
<i>Pleopeltis angusta</i> Humb. & Bonpl. ex Willd.	0	0	0	3
<i>Pleopeltis astrolepis</i> (Liebm.) E. Fourn.	0	0	0	0
<i>Pleopeltis lindeniana</i> (Kunze) A.R. Sm. & Tejero	53	39	100	100
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.	0	0	0	0
<i>Pleopeltis muenchii</i> (Christ) A.R. Sm.	33	26	61	87
<i>Pleopeltis plebeian</i> (Schltdl. & Cham.) A.R. Sm. & Tejero	0	0	0	0
<i>Pleopeltis</i> sp. 1	0	0	0	0
<i>Polypodium fissidens</i> Maxon	0	0	0	26
<i>Polypodium fraternum</i> Schltdl. & Cham.	0	0	0	5

1				
2				
3	<i>Polypodium plesiosorum</i> Kunze	0	0	0
4	<i>Polypodium pleurosorum</i> Kunze ex Mett.	11	1	48
5	<i>Polypodium polypodioides</i> var. <i>aciculare</i>			
6	Weath.	0	0	0
7				
8	<i>Polypodium rosei</i> Maxon	23	18	42
9	<i>Polypodium sanctae-rosae</i> (Maxon) C. Chr.	0	0	0
10				
11	<i>Polypodium</i> sp. 1	0	0	0
12	<i>Polypodium</i> sp. 2	17	13	31
13	<i>Polypodium subpetiolatum</i> Hook.	0	0	0
14				2
15	<i>Polystichum hartwegii</i> (Klotzsch) Hieron.	100	100	100
16	<i>Polystichum muricatum</i> (L.) Fée	0	0	17
17				33
18	<i>Polytaenium lineatum</i> (Sw.) J. Sm.	0	0	0
19				0
20	<i>Pteridium arachnoideum</i> (Kaulf.) Maxon	0	0	0
21	<i>Pteridium caudatum</i> (L.) Maxon	16	12	28
22	<i>Pteridium feei</i> (W. Schaffn. ex Fée) Faull	88	70	100
23	<i>Pteris orizabae</i> M. Martens & Galeotti	13	10	27
24	<i>Pteris pungens</i> Willd.	0	0	0
25	<i>Pteris vittate</i> L.	20	15	41
26				61
27	<i>Sceptridium decompositum</i> (M. Martens &			
28	Galeotti) Lyon	17	8	50
29	<i>Scoliosorus ensiformis</i> (Hook.) T. Moore	0	0	0
30				5
31	<i>Selaginella cladorrhizans</i> A. Braun	0	0	0
32	<i>Selaginella guatemalensis</i> Baker	0	0	0
33	<i>Selaginella pallescens</i> (C. Presl) Spring	0	0	0
34	<i>Selaginella pulcherrima</i> Liebm.	0	0	0
35	<i>Selaginella silvestris</i> Aspl.	39	30	72
36				100
37	<i>Serpocaulon dissimile</i> (L.) A.R. Sm.	16	2	68
38	<i>Serpocaulon triseriale</i> (Sw.) A.R. Sm.	0	0	0
39				0
40	<i>Sticherus</i> sp. 1	0	0	19
41	<i>Terpsichore asplenifolia</i> (L.) A.R. Sm.	0	0	0
42				31
43	<i>Thelypteris</i> sp.	0	0	0
44	unknown sp. 1	0	0	0
45	<i>Vandenboschia radicans</i> (Sw.) Copel.	0	0	0
46	<i>Vittaria graminifolia</i> Kaulf.	21	17	39
47	<i>Woodwardia spinulosa</i> M. Martens &			
48	Galeotti	0	0	13
49				42
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