

Diversity of epiphyte ferns along an elevational gradient in El Triunfo Biosphere Reserve, southern Mexico

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Background and aims – In the tropics, some studies have found that the richness of epiphytic ferns present a peak at mountain mid-elevations. However, it is not well understood how transitions from tropical to subtropical conditions affect this peak, and even less is known about beta diversity of epiphytic ferns. Thus, the objective is to understand the effect of climatic gradients on the variation of local richness of ferns and beta diversity patterns along an elevational gradient in a mountain system in southern Mexico.

Methods – We sampled 32 trees, each in four elevational bands (100–2200 m). Alpha diversity patterns were analysed using linear regression models. We used the Morisita index to quantify species turnover between bands. An additive partitioning approach was used to analyse the degree to which individual trees, plots, and bands contributed to total species richness. We evaluated the influence of climatic variables on species composition via linear regression models.

Key results – A total of 30 species in five families were recorded. Each family contributed in different magnitude to the elevational richness pattern, with Polypodiaceae dominating due to its richness and presence along the entire transect. Alpha diversity at the three scales (α_{tree} , α_{plot} , α_{band}) increased with elevation and rainfall, and with decreasing temperature. Species turnover was high along the gradient, but was scale-dependent, with β_{transect} (65–75%) and β_{band} (14%) with the greatest contributing to total diversity. Although the contribution of the individual trees was lower, it increased with elevation.

Conclusions – We emphasize the importance of including different scale levels in analyses of diversity along elevational gradients. In the region, cloud forest on the mountain peaks harbours the highest diversity of epiphytic fern communities. Due to a limited extent of this mountain range, the epiphyte ferns are susceptible to the effects of climate change.

Keywords – Alpha and Beta diversity; elevational pattern; fern richness; partitioning diversity; Sierra Madre de Chiapas.

INTRODUCTION

Patterns of species richness in mountain systems, and mechanisms determining them have received ample attention in ecological research (Rahbek 2005). For many groups of animals and plants, the diversity peak occurs at an intermediate point of the elevational gradient, but for others diversity shows continuous declines or other idiosyncratic diversity patterns (McCain 2005; Kreft et al. 2010). These diversity patterns have been shown to be influenced by topography, area, habitat heterogeneity, climate, edaphic conditions, evolutionary history, and human activities (Kluge et al. 2006; Jones et al. 2011; Karger et al. 2011; Tuomisto et al. 2014; Vetaas et al. 2019). Besides variation in species richness, taxonomic composition also changes with elevation, sometimes leading to distinct elevational zonation of biotic communities (Kessler 2000b; Peters et al. 2016).

Ferns are among the most prominent plant life forms in tropical montane forests. Of the about 11 000 species globally (PPGI 2016), roughly a quarter (2865 species) are epiphytic (Zotz 2013). Epiphyte ferns are best represented in environments with high humidity and low temperatures in tropical and subtropical ecosystems (Salazar et al. 2013), although globally fern diversity declines more strongly towards arid and cold climatic conditions than that of angiosperms (Kreft et al. 2010). Living mostly on trees, epiphytic ferns generally live under conditions of high light availability, but since they cannot access the soil, they suffer from shortages of water and nutrients (Benzing 1990). This has led to a wide range of morphological and physiological adaptations to optimize water and nutrient acquisition and storage (Benzing 1990; Schwerbrock & Leuschner 2017). For example, in some fern species, leaf scales can protect the fronds against solar radiation (Watkins et al. 2006) and the structure of trichomes probably influences the process of direct water absorption (Schwerbrock & Leuschner 2017). Particularly, filmy ferns of the family Hymenophyllaceae have leaves adapted to high humidity levels and low luminosity (Dubuisson et al. 2003), whereas the genus *Pleopeltis* has modified scales on the leaf epidermis that accelerate foliar re-hydration when environmental humidity increases (Kessler & Siorak 2007).

Epiphytic ferns typically show a hump-shaped pattern of species richness in relation to elevation, with maximum richness at mid-elevations (1300–2500 m) (Watkins et al. 2006; Kessler et al. 2011; Salazar et al. 2013; Carvajal-Hernández et al. 2017), although in some cases species richness increases with elevation (Bhattarai et al. 2004; Krömer et al. 2013). These elevational diversity patterns of epiphytic ferns have commonly been interpreted in relation to environmental factors, such as temperature, precipitation, and relative humidity (Kessler et al. 2011). Because of their life style, they are exposed to hydric stress, among others. While it seems intuitively appealing to link the diversity of epiphytic ferns to such factors, the actual mechanisms linking environmental conditions and diversity are still poorly understood (Kessler 2000a). For example, while epiphytic fern diversity is apparently strongly related to low temperatures and especially frost events (Krömer et al. 2005; Kreft et al. 2010), the question remains why so few species are able to survive under these conditions and what limits their ability to be represent-

ed by more than a few species. One approach to understanding such patterns is to contrast elevational diversity patterns of different plant groups with different physiological adaptations to be able to unravel the relationships of these adaptations to climate and richness patterns (McCain 2005).

In a broad sense, beta diversity is the variation in species composition between sampling units or communities in a spatial or environmental context (Whittaker 1960; Vellend 2001). Along elevational gradients, which are associated with marked climatic gradients, many groups of animals (Melo et al. 2009; Peters et al. 2016) and plants (Sánchez-González & López-Mata 2005; Krömer et al. 2013) show high levels of beta diversity. Among epiphytic ferns, little is known about elevational patterns of beta diversity, which becomes especially relevant since growth on individual trees potentially leads to high spatial variation in species composition (Gentry & Dodson 1987; Krömer et al. 2013). Understanding beta diversity is also of interest to conservation biology since it provides information about the impact of environmental and historical factors on spatial distribution of communities (Koleff et al. 2008).

To date, most studies on epiphyte fern diversity have been conducted in the tropics (e.g. Kessler 2001; Kluge et al. 2006; Watkins et al. 2006; Salazar et al. 2013), but little is known about the patterns at extremes tropical boundaries (Carvajal-Hernández & Krömer 2015; Carvajal-Hernández et al. 2017; Hernández-Rojas et al. 2018). Such is the case of southern Mexico, where the El Triunfo Biosphere Reserve (henceforth El Triunfo), located on the southern slope of the Sierra Madre de Chiapas, contains some of the most extensive and well-preserved montane forest tracts of northern Mesoamerica (Toledo-Aceves et al. 2011), characterized by high levels of diversity and species endemism (Rzedowski 1978). To date, 465 species of vascular epiphytes have been documented in El Triunfo (Martínez-Meléndez et al. 2009), contributing 15.5% of the local flora (Pérez-Farrera 2004). Of these species, 40 are regionally endemic and 28 are legally protected in Mexico (Martínez-Camilo et al. 2012). More than a quarter (134 species) of these epiphytes are ferns (Martínez-Meléndez et al. 2009). However, local patterns of epiphyte fern richness and how they vary with elevation have not yet been studied. In this study, we conducted a survey of epiphytic fern diversity along an elevational gradient in El Triunfo, focusing on the variation of local richness (alpha diversity) and compositional turnover (beta diversity) to address the following questions: (1) How do epiphytic fern diversity patterns (alpha and beta diversity) vary according to the different nested scales used to quantify them (host-tree, sampling plots, and elevational bands)? (2) How does climate affect the diversity patterns (alpha and beta diversity) of epiphytic ferns? and (3) How variable are these patterns among different families of ferns?

MATERIAL AND METHODS

Study site

El Triunfo Biosphere Reserve is located in the middle part of the Sierra Madre de Chiapas (fig. 1) in southeastern Mexico. The reserve covers an area of 119 117 ha and altitude ranges

from sea level to over 3000 m on the local mountain peaks. Climatic conditions range from humid, hot lowlands to humid, cool highlands, with annual total rainfall ranging from 2500 to 4000 mm, depending on elevation and exposure to incoming rain fronts from the Pacific (Galindo-Jaimes 2008). Vegetation consists of tropical rain forests at low elevations, lower montane rain forest in the intermediate parts, and cloud forest or montane rainforest at high elevations (Breedlove 1981). El Triunfo is one of the most important conservation areas in Mexico due to the large tracts of cloud forest and numerous conservation activities that are mainly funded by payments for ecosystem services, and because it is one of the most important coffee-growing areas in the country, including organic production (Cortina-Villar et al. 2012).

Data collection

Due to topographic complexity and accessibility, we conducted the survey in four distinct elevational bands: low (100–300 m), middle-low (700–900 m), middle-high (1300–1500 m), and high (1900–2200 m). In each band, we established four 0.1 ha circular plots at least 100 m apart. The sampling plots were located in the best preserved forest stands avoiding canopy gaps. In lower bands, most of the plots were located in isolated old growth forest patches and in mid-successional secondary stands. At high elevations, plots were located in the nucleus zone of the Triunfo

reserve (Martínez-Camilo et al. 2018). We avoided steep sites ($> 35^\circ$ inclination) due to difficult accessibility. In each plot, we selected eight trees distributed proportionally in the cardinal directions. This resulted in a sample of 32 trees per band, and a total of 128 sampled trees. Since epiphyte diversity and assemblage composition are known to be influenced by tree size and species identity (Flores-Palacios & García-Franco 2006), sampled trees with a diameter at breast height (dbh) of 40–140 cm were selected to represent the range of the most common canopy tree species at each elevation. Field work was carried out May to December 2014.

We recorded the presence-absence of all species, excluding small juveniles because they could not be identified (Sanford 1968). We recorded epiphytic ferns for each tree in the field using binoculars, and when necessary, trees were accessed via single-rope climbing techniques (Perry 1978). We focused our surveys on the epiphytic ferns, according to the classification of PPGI (2016). All species were collected for later determination based on Mickel & Smith (2004) and consulted specialists (see acknowledgments). Specimens were deposited in the herbarium HEM of the Universidad de Ciencias y Artes de Chiapas, Tuxtla Gutierrez. Because we were not able to identify all species at species level, especially in the case of sterile plants, 13.3% of the species are listed only at genus level. To determine the conservation sta-

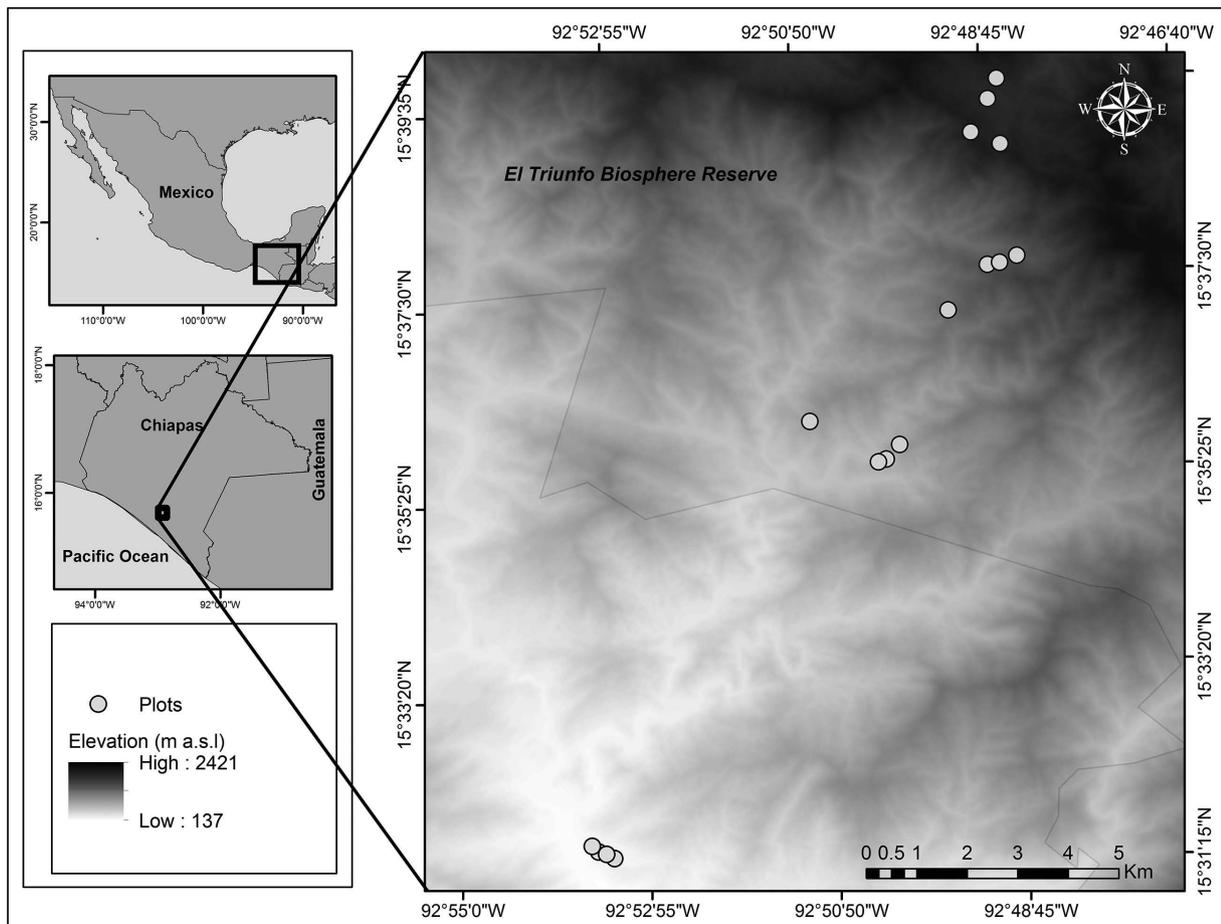


Figure 1 – Location of the study sites in the El Triunfo Biosphere Reserve.

tus of each species, we consulted the Risk List of the Norma Oficial Mexicana (SEMARNAT 2018).

Environmental variables

To relate diversity patterns to environmental conditions, we obtained the following data. We included elevation as a topographic variable, measured in the center of each 0.1 ha plot with a Garmin® Etrex 30x GPS. We further included two climatic variables that have commonly been linked to epiphytic ferns (Kessler et al. 2011), namely total annual rainfall and mean annual temperature, based on the CHELSA climate base (Karger et al. 2017). This database provides climatic information at a spatial resolution of about 1 km², covering 39 years of data. Compared with other similar global climatic databases, CHELSA has improved predictive power in mountainous regions with limited station data (Karger et al. 2017).

Data analysis

We calculated alpha diversity as true diversity (numbers equivalents; Jost 2007). Values of alpha diversity were calculated for all of epiphytic fern families combined for the transect at three spatial scales: alpha tree diversity (total richness in each tree: α_{tree}), alpha plot diversity (mean of the eight trees per plot: α_{plot}), and alpha elevational band diversity (mean of the four plots per band: α_{band}). Elevational patterns of alpha diversity values were assessed via regression models. Furthermore, we calculated alpha diversity for each elevational band at the same three spatial scales (α_{tree} , α_{plot} and α_{band}).

We studied beta diversity with two complementary approaches: species turnover and additive partitioning. To assess species turnover, we calculated the Morisita similarity index, based on incidence / frequency data (number of records of a species on a tree) between elevational bands. This index ranges from 0, when the sites are identical in their species composition, to 1, when they are totally dif-

ferent (Magurran 2004; Chao et al. 2008), using the spadeR package (Chao et al. 2016; R Core Team 2018). In addition, we calculated additive beta partitioning, first calculating the mean richness at each of the three sampling scales (α_{tree} , α_{plot} and α_{band}) and then by partitioning the relative contribution of each of scales by calculating $\beta_{plot} = \alpha_{plot} - \alpha_{tree}$; $\beta_{band} = \alpha_{band} - \alpha_{plot}$, and $\beta_{transect} = \gamma - \alpha_{band}$ (Veech et al. 2002, Crist et al. 2003; Jost 2007), where γ corresponds to the 30 species counted overall (gamma diversity). Finally, we calculated the partitioning diversity (alfa and beta) for each family to observe their elevational diversity pattern.

We evaluated the relative influence of the variables elevation, annual total rainfall, and mean annual temperature via linear regression models. Prior to running the tests, we used the Pearson test to evaluate covariance between variables, finding high collinearity for all factors (rainfall vs. elevation, $R^2 = 0.87$, $P < 0.001$; temperature vs. elevation, $R^2 = -0.99$, $P < 0.001$ rainfall vs. temperature, $R^2 = -0.89$, $P < 0.001$). Thus, we excluded elevation as an independent factor, considering that precipitation and especially temperature reflect elevation along our study gradient. For all tests, we used a significance threshold of 0.05 ($P < 0.05$). All analyses were run on the platform R (R Core Team 2018).

RESULTS

Composition and species in risk categories

In total, we recorded 30 species of epiphytic ferns belonging to five families. The most species rich families were Polypodiaceae (19), followed by Hymenophyllaceae (4), and Dryopteridaceae (3) (supplementary file 1). Only one family was recorded in the lowest elevational band, two families in the middle-low, three in the middle-high, and five in the high bands (fig. 2). The relative contribution of families to overall richness within each elevational band varied accordingly, with Polypodiaceae contributing 100% of all species in the low elevated band but less than 50% in the high elevated

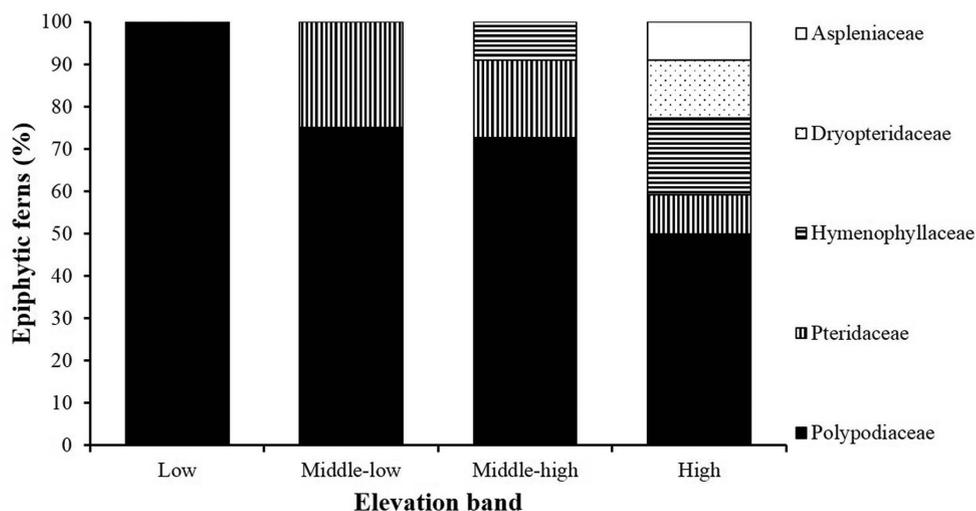


Figure 2 – Taxonomic composition of epiphyte fern assemblages along an elevational gradient in El Triunfo Biosphere Reserve, Mexico.

band. In contrast, the contribution of Hymenophyllaceae increased from less than 10% to over 18% in the middle-high elevated band, and the families Aspleniaceae and Dryopteridaceae were recorded only in the high elevated band (fig. 2). Regarding the conservation status, and according to the NOM-059-SEMARNAT-2018 (SEMARNAT 2018), only one species, *Serpocaulon triseriale* (Sw.) A.R.Sm, is categorized as threatened.

Patterns of alpha diversity

The means of alpha diversity were dependent on spatial scale and elevation (table 1). At the tree level, highest diversity was recorded in the high band, with 8.5 species on average, whereas in the low band, we only recorded 0.09 species on average. At plot and band scale, diversity values were lowest in the low band (0.25 and 2 species, respectively), with highest values in the high band (13.46 and 22, respectively) (table 1). Alpha diversity values at the three scales (α_{tree} , α_{plot} , α_{band}) showed similar patterns of increase with elevation, for the overall data set ($R^2 = 0.71$, $P < 0.001$, $R^2 = 0.89$, $P < 0.001$, and $R^2 = 0.98$, $P < 0.001$, respectively) (fig. 3). At family level, we also observed an increase of diversity with elevation. Overall, the diversity patterns were largely driven by the family Polypodiaceae, which contributed two thirds of the species richness, along the entire gradient, whereas the families Aspleniaceae, Dryopteridaceae, and Hymeno-

Table 1 – Paired complementarity matrix of the Morisita index between the elevational belts along the study transect, based on species frequencies.

1 indicates identical assemblages and 0 total dissimilarity (Chao et al. 2008).

Elevation band	Low	Middle-low	Middle-high
Low			
Middle-low	0.42		
Middle-high	0	0.55	
High	0	0.19	0.05

phyllaceae were only recorded in the middle and high bands (supplementary file 1). Linear regression models showed that overall species richness of epiphyte ferns increased with increasing rainfall ($R^2 = 0.6$, $P < 0.001$) and with decreasing temperature ($R^2 = 0.65$, $P < 0.001$) (fig. 4).

Patterns of beta diversity

The Morisita index revealed a low level of similarity among elevational bands, with complete turnover between the low and high bands (table 2). However, even the middle-high and high bands were highly distinct from each other ($P < 0.05$). This was also reflected by the additive partitioning approach,

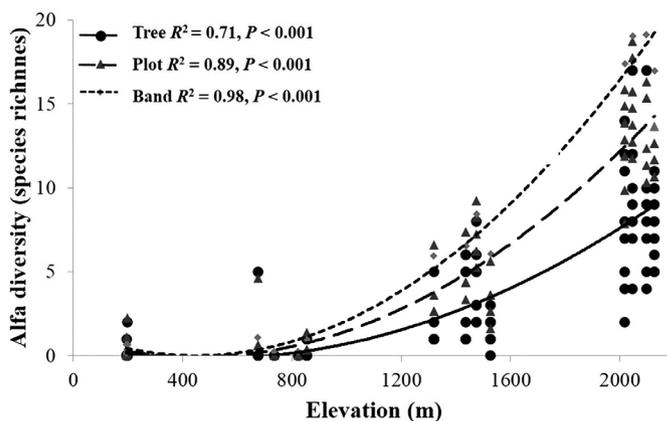


Figure 3 – Species richness patterns (alpha diversity) of epiphyte ferns along an elevational gradient in El Triunfo Biosphere Reserve, Mexico, at three spatial scales (tree: dots and continuous line; plot: triangles and long-dashed lines; transect: diamond and long-dashed lines).

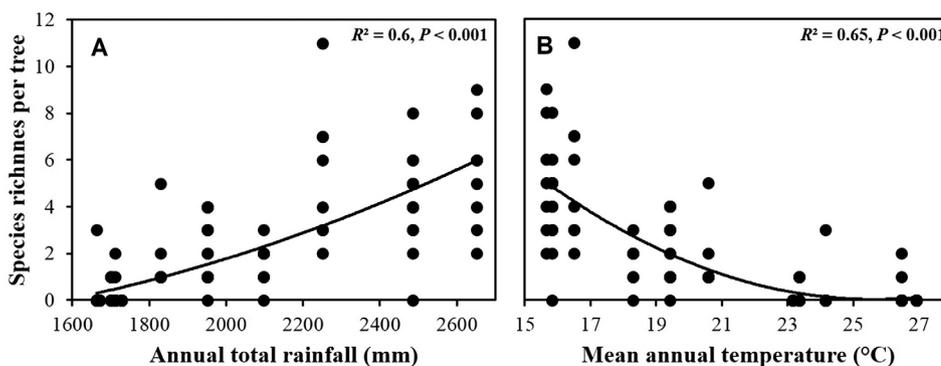


Figure 4 – Pattern of richness distribution of epiphyte ferns in relation to rainfall and temperature in El Triunfo Biosphere Reserve, Mexico.

which showed, for all groups, that 65–75% of the overall beta diversity was due to differences between bands (β_{transect}), except for Pteridaceae in the high elevation band, where this value was 37.5% (fig. 5). On average, single trees (α_{tree}) contained about 7% of the overall epiphytic ferns diversity of the entire transect, whereas β_{plot} contributed about 13% to total diversity and β_{band} 14%.

DISCUSSION

This is the first study to describe the variation of local species richness and turnover of epiphyte ferns in the transition between the tropical and subtropical region in Mesoamerica. Our main results show an overall elevational increase of epiphytic fern richness and marked species turnover along the gradient, especially between the high elevation band and the other three bands.

Composition and species in risk categories

In total, we recorded 30 species of epiphytic ferns on the 128 studied trees; representing 22.38% and 45.45% of the species and families, respectively, of the epiphytic ferns known in El Triunfo, and 6.45% and 16.12 % of the species and families, respectively, of the vascular epiphytes known in El Triunfo (Martínez-Meléndez et al. 2009). The abundance of the family Polypodiaceae is typical for subtropical forest habitats (Wolf & Flamenco 2003; Carvajal-Hernández & Krömer 2015; Acebey et al. 2017; Hernández-Rojas et al. 2018) and contrasts with very humid tropical sites in the Andes, where Dryopteridaceae and Hymenophyllaceae are the most diverse (Kessler 2000a; Kluge et al. 2006; Bach et al. 2007). In our study, these two families were restricted to habitats with high levels of air moisture and low luminosity as is typical

for cloud forests, in the high parts of the gradient (Benzing 1990; Dubuisson et al. 2003; Cardelús & Mack 2010; Proctor 2012). Dryopteridaceae and Hymenophyllaceae have rhizomes fine to filiform and leaves adapted to high humidity levels (Dubuisson et al. 2003), whereas ferns of the Polypodiaceae have thick, water- and nutrient-storing rhizomes and are often poikilohydric (Sundue et al. 2015). Although our study region is one of the most humid in Mexico, it experiences occasional periods of low precipitation (Escalante-Sandoval & Amores-Rovelo 2014), and it is tempting to relate the high diversity of Polypodiaceae to their ability to withstand drought conditions. Overall, both edaphic and climatic variation are important determinants of community structure of ferns (Lehtonen et al. 2015). Here, aspects of their evolutionary history may be key to understanding regional variation in species richness, as that diversification rates in some groups of ferns are positively correlated with changes in elevation (Dubuisson et al. 2003; Graham 2010; Kessler et al. 2011; Sundue et al. 2015; Lehtonen et al. 2017).

While we only recorded a single species that is considered to be threatened at the national scale, namely *Serpocaulon triseriale* (Sw.) A.R.Sm., a species widely distributed from Mexico to southern Brazil (Mickel & Smith 2004; GBIF 2019), it may be interesting to note that it was only recorded in the middle and high elevation bands where cloud forests are predominant, which is the most threatened vegetation type in México (González-Espinosa et al. 2012). This was also the vegetation type where we recorded the highest diversity of species and families. This pattern has also been found in other areas in Mexico (Martínez-Meléndez et al. 2009; Carvajal-Hernández & Krömer 2015).

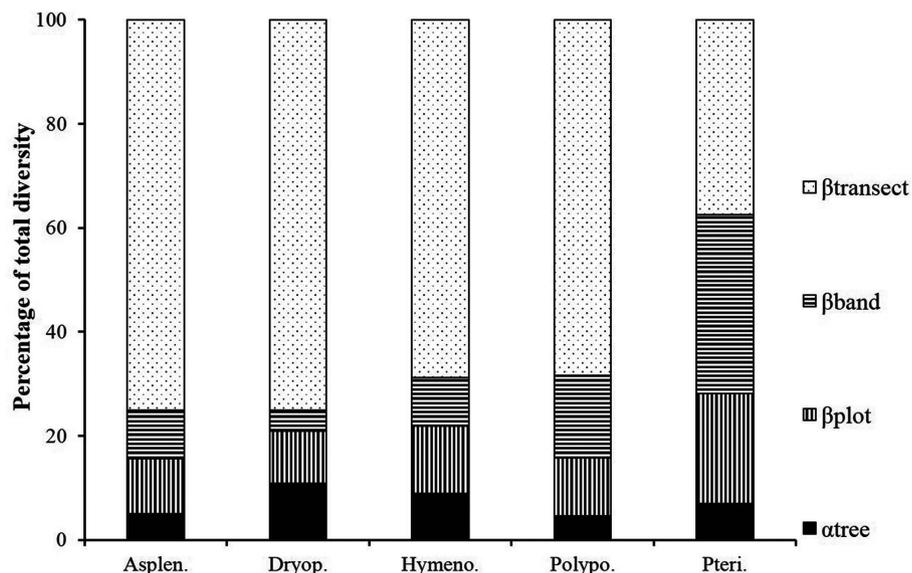


Figure 5 – Diversity partitioning among the epiphyte ferns along an elevational gradient in El Triunfo Biosphere Reserve, Mexico. α_{tree} corresponds to the mean number of species per tree along the entire transect, β_{plot} to the additional number of species encountered when one studies all 8 trees of a plot, β_{band} to the additional species when studying all 4 plots per band, and β_{transect} to the additional number of species encountered along the whole transect. Asplen. = Aspleniaceae; Dryopt. = Dryopteridaceae; Hymeno. = Hymenophyllaceae; Polypo. = Polypodiaceae; Pteri. = Pteridaceae.

Patterns of alpha diversity

We found an increase in species richness with elevation at the three spatial scales (α_{tree} , α_{plot} by α_{band}), which is the most frequent pattern up to elevations of about 2000–2500 m and has also been reported from other elevational transects in the tropics (Kessler 2000a, 2001; Kluge et al. 2006; Salazar et al. 2013), as well as in the transition from the tropics to subtropics (Krömer et al. 2013; Carvajal-Hernández & Krömer 2015; Acebey et al. 2017; Carvajal-Hernández et al. 2017; Hernández-Rojas et al. 2018). Above this altitude local diversity decreases in both the Neotropics in general (Cardelús et al. 2006; Kessler et al. 2011; Salazar et al. 2013) and Chiapas in particular (Wolf & Flamenco 2003). In our study region, the highest local diversity was found in the high elevation belt, which corresponds to a humid cloud forest vegetation where regular fog condensation, in addition to the high levels of rainfall, increases humidity. This relationship of high local diversity of epiphytic ferns in habitats with high air humidity has commonly been found and has been related to the water requirements of plants and epiphytes in general (Benzing 1990; Gentry & Dodson 1987; Vetaas et al. 2019) and of ferns in particular (Kessler et al. 2011).

Patterns of beta diversity

We found high levels of species turnover among elevational belts, especially between the highest belt and the other three. This turnover was mainly explained by variation in precipitation, rather than by temperatures (Tuomisto et al. 2014). Additional factors may be less logging activities in the cloud forest, which would affect the tallest trees with the richest assemblages of epiphytic ferns (Wang et al. 2003; Kluge et al. 2006), greater habitat heterogeneity due to topographical complexity and associated microclimatic differences (Kessler 2001; Krömer et al. 2005), as well as edaphic and climatic conditions (Jones et al. 2008, 2011; Tuomisto et al. 2014). This reveals that there is a fundamental distinction between the diverse epiphytic ferns found in the humid cloud forest above 1800 m and the epiphyte floras at lower elevations, which, although located in evergreen rainforests, receive less water input through fog (Wolf & Flamenco 2003; Küper et al. 2004). In fact, the lower level of regular cloud condensation in the study region appears to be very regularly located between about 1800–2200 m, creating a rather abrupt change of vegetation type at this elevation, which is clearly reflected in the in general epiphyte communities. On the other hand, we also observed high levels of taxonomic turnover in the lower three belts, reflecting typical species turnover with elevation, which has been estimated at around 10% for each 100 m in elevation (Kessler 2000b), roughly corresponding to the values we observed.

CONCLUSION

Our study has implications for the conservation of epiphyte flora, in general, in southern Mexico. In particular, the high diversity and distinctness of the cloud forest flora must be stressed (González-Espinosa et al. 2012). Considering that global climate change is expected to result in widespread upward shifts of cloud condensation layers (Foster 2001; Lawton et al. 2001) and that the mountains of the El Triunfo

area mostly do not exceed 2500 m, the already narrow cloud forest belt can be expected to narrow even further, without the possibility for species to shift upwards. This situation has already been observed elsewhere and has been linked with massive losses of biodiversity (Pounds et al. 1999; Nair et al. 2003). On the other hand, direct human impact via deforestation and agriculture is most severe at lower elevations (Martínez-Camilo et al. 2018), where it may threaten epiphyte floras in general, as also observed elsewhere (e.g. Köster et al. 2009).

SUPPLEMENTARY FILE

One supplementary file is associated to this paper:

Checklist of species (1 = presence, 0 = absence) found in each elevational belt at El Triunfo Reserve Biosphere, Mexico:

<https://doi.org/10.5091/plecevo.2020.1573.1949>

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