

# Effects of forest-use intensity on vascular epiphyte diversity along an elevational gradient

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## Funding information

Deutscher Akademischer Austauschdienst, Grant/Award Number: 91570360

Editor: Marion Pfeifer

## Abstract

**Aim:** Understanding patterns of tropical plant diversity and their vulnerability to anthropogenic disturbance at different spatial scales remains a great challenge in ecology and conservation. Here, we study how the effects of forest-use intensity on vascular epiphyte diversity vary along a tropical elevational gradient.

**Location:** 3,500-m elevational gradient along the eastern slopes of Cofre de Perote, Mexico.

**Methods:** We studied the effects of forest-use intensity on alpha, beta and gamma diversity of vascular epiphyte assemblages in old-growth, degraded and secondary forests at eight study sites at 500-m intervals along the elevational gradient. At each elevation and in each of the three forest-use intensity levels, we established five 400-m<sup>2</sup> plots yielding a total of 120 plots.

**Results:** Interactive effects of elevation and forest-use intensity strongly impacted local-scale patterns of vascular epiphyte diversity. Species diversity peaked at 500 m as well as 1,500 m above sea level, which deviates from the previously reported hump-shaped pattern. In most cases, alpha diversity did not differ significantly among forest-use intensity levels. However, gamma diversity was always lower in secondary forests compared to old-growth forests across the entire elevational gradient. Within each elevational belt, beta diversity was dominated by species turnover along the forest-use intensity gradient in the lowlands and declined with increasing elevation, where community composition became increasingly nested. Along the elevational gradient, the spatial turnover of vascular epiphyte community composition was similar among forest-use intensity levels.

**Main conclusions:** Our results reveal a strong interaction between forest-use intensity and elevation, making it difficult to extrapolate findings from one elevational belt to another. Our findings highlight the value of old-growth forest for epiphyte diversity, but also show that degraded and secondary forests—depending on the elevational belt—may maintain a high species diversity and thus play an important role in conservation planning.

## KEYWORDS

beta diversity, bromeliads, composition, disturbance, elevation, ferns, forest-use, orchids, species richness, tropical vegetation

## 1 | INTRODUCTION

Tropical forests are estimated to host over half of all global terrestrial biodiversity (Pimm & Raven, 2000), yet are being rapidly lost due to deforestation and land-use change (Gibson et al., 2011; Newbold et al., 2015). Understanding the current status of tropical biodiversity and developing effective conservation and management strategies thus depends on improving our understanding outside of intact forest reserves (Chazdon, Harvey, et al., 2009) and the role of human-modified forests for conservation. Despite recent progress (Newbold et al., 2015; Peters et al., 2019), our knowledge of how forest-use intensity affects tropical biodiversity along natural environmental gradients remains limited.

Ecological patterns are often studied along elevational gradients, which provide the opportunity to study effects of different ecological and evolutionary factors on biodiversity patterns over relatively short geographical distances (Körner, 2007). Climate (e.g. temperature and precipitation) usually plays a fundamental role in shaping diversity patterns along elevational gradients (McCain & Grytnes, 2010; Peters et al., 2019). However, different levels of forest disturbance should also play an important role in mediating microclimatic changes at local scales, which in turn may affect species diversity, especially life forms that are sensitive to air humidity and temperature, such as vascular epiphytes (Larrea & Werner, 2010; Werner & Gradstein, 2009; Zotz & Bader, 2009). Most studies investigating the distribution and diversity of vascular epiphytes along tropical elevational gradients report a hump-shaped pattern, with a peak in species diversity at mid-elevations (e.g. Acharya, Vetaas, & Birks, 2011; Bhattarai, Vetaas, & Grytnes, 2004; Cardelús, Colwell, & Watkins, 2006; Ding et al., 2016; Gentry & Dodson, 1987; Hietz & Hietz-Seifert, 1995; Kluge, Kessler, & Dunn, 2006; Krömer, Kessler, Gradstein, & Acebey, 2005; Salazar et al., 2015). The shape of this pattern is thought to be driven by humidity and temperature, which are at optimal levels for vascular epiphytes at mid-elevations (Bhattarai et al., 2004; Kluge et al., 2006).

Forest-use intensity and anthropogenic disturbance might negatively affect vascular epiphyte diversity in human-modified landscapes (Barthlott, Schmit-Neuerburg, Nieder, & Engwald, 2001; Köster, Friedrich, Nieder, & Barthlott, 2009; Krömer & Gradstein, 2003). Depending on the degree (e.g. severity and/or frequency) of forest disturbance, species composition might also change, with some epiphytic taxa being more affected than others (Flores-Palacios & García-Franco, 2004; Hietz, Buchberger, & Winkler, 2006; Larrea & Werner, 2010). Effects of forest disturbance on vascular epiphyte diversity have also been attributed to isolation and time effects, due to site-specific factors that affect seed availability, dispersal and recovery (Cascante-Marín et al., 2006). The younger age

and reduced structural complexity of host trees in secondary forests may further limit the availability of different microhabitats that vascular epiphytes can colonize within a host tree (Hietz & Briones, 1998; Krömer & Gradstein, 2003; Taylor & Burns, 2015), depending on their preference for darker and more humid lower canopy or more sun-exposed branches in the upper canopy (Hietz, 1998; Krömer, Kessler, & Gradstein, 2007). Reduced structural complexity of the canopy might further reinforce changes in the microclimate, resulting in a less pronounced vertical zonation within the tree (Böhnert et al., 2016), higher drought stress and an overall decrease in a host tree's suitability for certain species (Krömer & Gradstein, 2003; Werner, Homeier, & Gradstein, 2005). Nevertheless, while some groups of vascular epiphytes in tropical cloud forests may be negatively affected by decreased humidity (e.g. orchids, filmy and grammitid ferns), more drought-resistant species (e.g. xeromorphic bromeliads) may benefit from the novel climatic conditions generated by land-use change (Barthlott et al., 2001; Krömer, García-Franco, & Toledo-Aceves, 2014; Zotz & Bader, 2009). To date, however, the joint effects of forest-use intensity and elevation on vascular epiphyte diversity patterns have not been examined.

Assessing how diversity patterns vary across multiple spatial scales has the potential to deepen current understanding of the consequences of disturbance on species diversity and composition in human-dominated tropical landscapes. In their seminal paper, Gentry and Dodson (1987) hypothesized that the high alpha and gamma diversity of Neotropical vascular epiphytes is due to niche partitioning along environmental gradients, which implies high beta diversity (i.e. spatial variation in composition), a component of diversity that remains poorly studied in vascular epiphytes. In this regard, analysing beta diversity and its nestedness and turnover components offers a compelling framework to understand the contribution of historical and ecological factors that may determine diversity patterns (Baselga, 2010). The nestedness component of beta diversity captures to what extent the assemblage with a lower number of species is a subset of an assemblage with higher number of species (Ulrich & Gotelli, 2007). Nestedness may be the dominant component of beta diversity in disturbed ecosystems, in which increasing land-use intensity reduces the number of species that can persist. The species turnover component of beta diversity, in contrast, reflects the replacement or change in species composition across ecological gradients (Baselga, 2010; Qian, Ricklefs, & White, 2005), where environmental filtering excludes species that do not have adaptive traits for establishing in particular parts of the gradient (Kraft et al., 2015). Therefore, the relative contribution of the nestedness and turnover components to beta diversity may reveal ecological mechanisms that determine how the composition of vascular epiphyte communities varies with elevation and forest-use intensity.

Here, we investigate how vascular epiphyte diversity at local to landscape scales responds to different levels of forest-use intensity (FUI) along a 3500-m elevational gradient within the Mesoamerica biodiversity hotspot (Albuquerque, Benito, Beier, Assunção-Albuquerque, & Cayuela, 2015; Brooks et al., 2002). We were interested in determining whether effects of FUI on species diversity patterns varied along the elevational gradient, which we addressed with the following questions: (a) Does the diversity of vascular epiphytes follow a hump-shaped pattern with a mid-elevation peak? (b) How is species diversity affected by FUI, and does this vary with elevation? (c) To what extent do FUI and elevation alter spatial variation in beta diversity? We expected vascular epiphyte diversity to peak at mid-elevations (Cardelús et al., 2006; Krömer et al., 2005) and FUI to reduce species diversity (Nöske et al., 2008; Wolf, 2005) and to influence beta diversity via the nestedness component more than turnover by reducing the size of the species pool. Moreover, we anticipated that elevation would have stronger effects on the turnover component of beta diversity, reflecting environmental filtering processes (Myers et al., 2013; Socolar, Gilroy, Kunin, & Edwards, 2016).

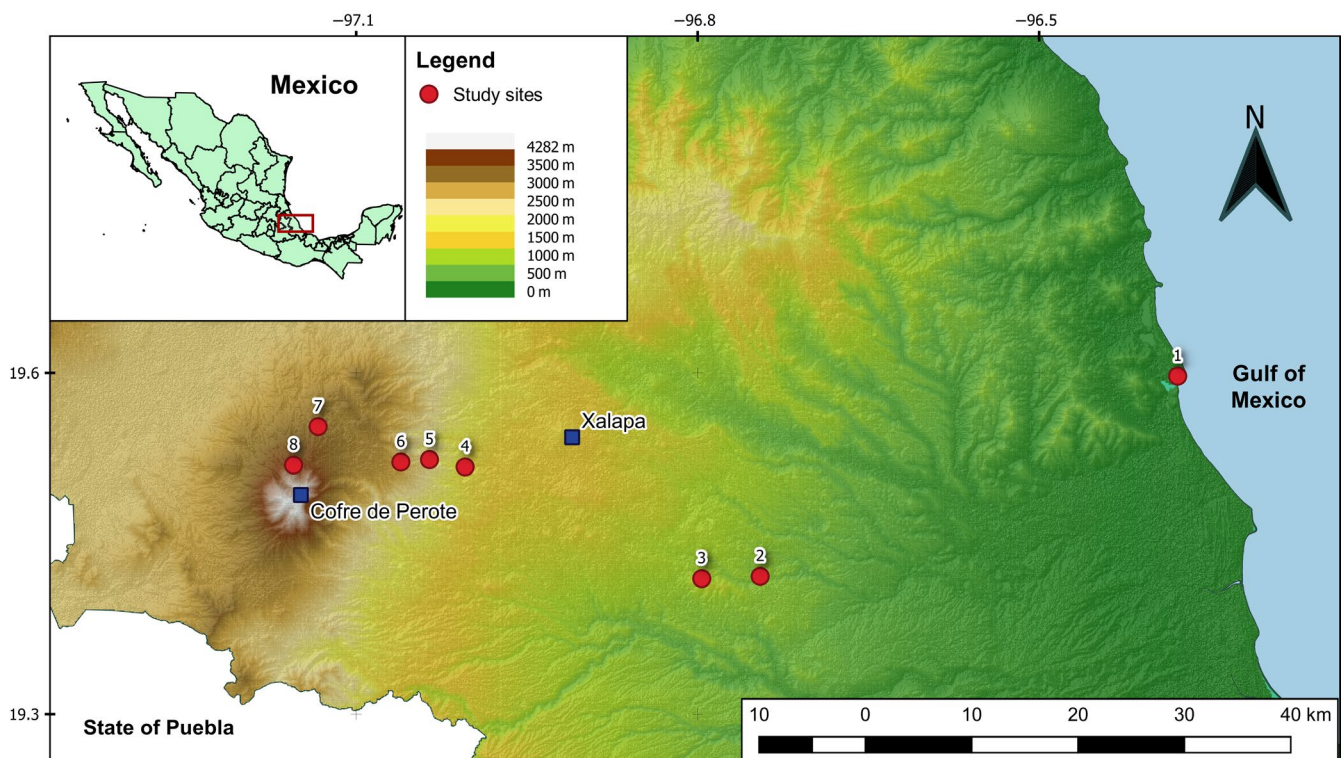
## 2 | METHODS

### 2.1 | Sampling design

We studied vascular epiphyte diversity along an elevational gradient from sea level to 3,500 m on the eastern slopes of Cofre de Perote, a

4,282 m high extinct volcano located in the central part of Veracruz State, Mexico (Figure 1). In this region, the Trans-Mexican volcanic belt and the Sierra Madre Oriental converge, combining floristic elements from the Nearctic and Neotropics. The climate in the study region ranges from dry-hot in the lowlands (mean annual temperature (MAT): 25°C; mean annual precipitation (MAP): 1,222 mm) to humid-temperate at mid-elevations (MAT: 13–19°C; MAP: 2,952–1,435 mm) and dry-cold at high elevations (MAT: 9°C; MAP: 708 mm; data according to the National Meteorological Service of Mexico 1951–2010). Along this gradient, six main vegetation types are present (Carvajal-Hernández & Krömer, 2015): (1) semi-humid deciduous forest at 0–700 m, (2) tropical oak forest at 700–1,300 m, (3) humid montane forest at 1,300–2,400 m, (4) pine-oak forest at 2,400–2,800 m, (5) pine forest at 2,800–3,500 m and (6) fir forest at 3,500–3,600 m (Table 1).

The current conservation status of the natural forests in this region is critical. More than 80% of the forests have been converted to pastures, plantations and secondary forests (Ellis, Martínez-Bello, & Monroy-Ibarra, 2011; Gómez-Díaz et al., 2018). Consequently, the remaining forests are highly fragmented and subjected to ongoing disturbance and deforestation for agriculture, cattle ranching and extraction of timber and non-timber forest products. We investigated three levels of forest-use intensity (FUI) that could be consistently found along the entire gradient following (Gómez-Díaz et al., 2017): (1) old-growth forests (OG) encompass mature forests with no or little signs of logging and other human impacts, classified as the lowest FUI; (2) degraded forests (DF) were defined as forests with clear signs of previous logging, sometimes with ongoing cattle grazing, removal



**FIGURE 1** Eastern slopes of the Cofre de Perote mountain in the state of Veracruz, Mexico. Red dots indicate the eight study sites (Table 1). Blue squares indicate summit of the Cofre de Perote mountain, and the city of Xalapa as reference points

**TABLE 1** Locations and climatic conditions of the eight study sites along the elevational gradient at the Cofre de Perote, central Veracruz, Mexico

Site	Elevation range (m)	MAT (°C)	MAP (mm/a)	Canopy height (m)	N latitude	W longitude	Vegetation type
1	0–45	26	1,222	~33	19.59	–96.38	Semi-humid deciduous forest
2	610–675	23	946	~34	19.41	–96.74	Semi-humid deciduous forest
3	980–1,050	21	1,331	~38	19.41	–96.79	Tropical oak forest
4	1,470–1,700	19	1,436	~53	19.52	–96.98	Humid montane forest
5	2,020–2,200	14	2,952	~47	19.50	–97.03	Humid montane forest
6	2,470–2,600	12	1,104	~42	19.52	–97.05	Pine-oak forest
7	3,070–3,160	9	708	~30	19.55	–97.13	Pine forest
8	3,480–3,545	9	708	~32	19.51	–97.16	Fir forest

Note: Elevational range, vegetation type according to Carvajal-Hernández and Krömer (2015), mean annual temperature (MAT) (°C) and mean annual precipitation (MAP) (mm/a) according to the National Meteorological Service of Servicio Meteorológico Nacional (SMN, 2016). Data cover 1951–2010.

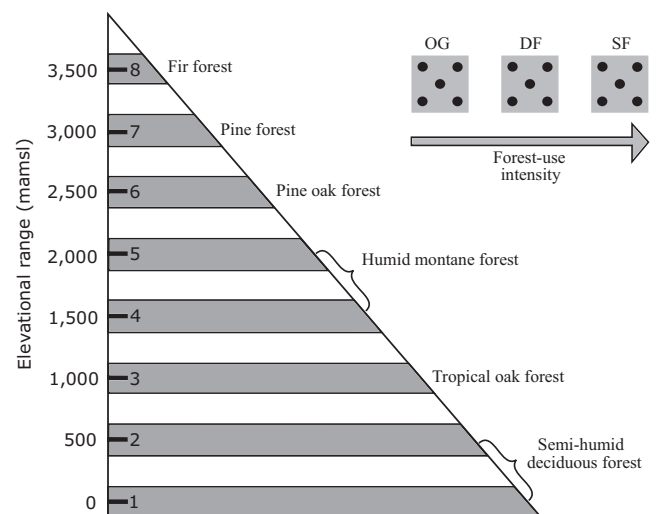
of understory and/or harvesting of non-timber forest products, classified as intermediate FUI; and (3) secondary forests (SF) were young forests at an intermediate successional stage of 15–25 years after abandonment (based on explanations by the land-owners), often with signs of continued human impacts, such as the removal of understory vegetation, non-timber forest products or partial tree cutting and occasional cattle grazing, classified as high FUI.

## 2.2 | Data collection

We selected eight study sites each separated by c. 500 m along the elevational gradient with the following elevational ranges (Table 1): 0–45 m, 610–675 m, 980–1,050 m, 1,470–1,700 m, 2,020–2,200 m, 2,470–2,600 m, 3,070–3,160 m and 3,480–3,545 m (hereafter referred to as 0, 500, 1,000, 1,500, 2,000, 2,500, 3,000, 3,500 m). At each study site, we surveyed vascular epiphytes in five non-permanent 20 m × 20 m plots for each of the three FUI levels (Figure 2), respectively, from July 2014 to May 2015. This yielded a total number of 120 plots. Vascular epiphytes were surveyed following the sampling protocol of Gradstein, Nadkarni, Krömer, Holz, and Nöske (2003). First, ground-based surveys were conducted; each plot was divided in four quadrants to better record the presence of epiphyte assemblages in the forest understory up to a height of ~8 m (Krömer et al., 2007), using collecting poles and binoculars (Flores-Palacios & García-Franco, 2001). Second, one mature host tree per plot was chosen by its size, health and crown structure for safe canopy access. We climbed from the base to the outer portion of the tree crown using the single-rope climbing technique (Perry, 1978) and examined each of the five Johansson zones for vascular epiphytes, which are frequently used to describe the spatial distribution of vascular epiphytes in tree canopies (Johansson, 1974; Sanger & Kirkpatrick, 2017). For each plot, we recorded the frequency of each species as the sum of incidences in the four subplots and the host tree (max. frequency per plot = 5). We used a Garmin® GPSMAP 60Cx device (Garmin International, Inc. Kansas, USA) to record geographical coordinates and elevation of all plots.

Vascular epiphytes were first identified as morphospecies in the field and collected, if possible, in triplicate to be preserved as

herbarium specimens. These specimens were identified using relevant literature (Croat & Acebey, 2015; Espejo-Serna, López-Ferrari, & Ramírez-Morillo, 2005; Hietz & Hietz-Seifert, 1994; Mickel & Smith, 2004) and by comparison with specimens deposited at the National Herbarium (MEXU), Universidad Nacional Autónoma de México, in Mexico City, and the herbarium of the Institute of Ecology (XAL) in Xalapa, Veracruz. Some taxa were sent to specialists for identification, namely Crassulaceae (Dr. Pablo Carrillo Reyes, Universidad de Guadalajara), Cactaceae (Dr. Miguel Cházaro Bazáñez, Universidad Veracruzana), Bromeliaceae and Orchidaceae (Dr. Adolfo Espejo-Serna and MSc. Ana Rosa López-Ferrari, Universidad Autónoma de México, Iztapalapa), Pteridophytes (Dr. Alan Smith, UC Berkeley) and *Peperomia* (Guido Mathieu, Botanic Garden Meise, Belgium). Species not identified to species level were assigned to morphospecies, using



**FIGURE 2** Schematic diagram illustrating the sampling design along the elevational gradient. Eight study sites were placed at every 500 m in elevation (numbered 1 to 8), and the respective vegetation type is given (following each section of the elevation). Forest-use intensity at each study site is represented with five plots each in old-growth forest (OG), degraded forest (DF) and secondary forest (SF) (total  $n = 120$  plots)

the genus or family name followed by the registered elevation and a consecutive number. The collection of protected species mentioned in Mexican law was facilitated by a plant collection permit (NOM-059-SEMARNAT-2010) issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT SGPA/DGVS/2405/14). All species names follow The Plant List version 1.1 (2013).

## 2.3 | Data analysis

### 2.3.1 | Species diversity

We estimated plot-level species diversity using Hill numbers (Chao et al., 2014) in terms of the effective numbers of species to facilitate comparisons across elevations and FUI levels (Jost, 2006). As we recorded species incidences in plots and Johansson zones rather than abundances, we used incidence-based diversity estimators following Chao et al. (2014). In this framework (Chao & Jost, 2012),  $q = 0$  ( ${}^0D$ ) is species richness and gives equal weight to frequent and infrequent species;  $q = 1$  ( ${}^1D$ ) is Shannon diversity and gives more weight to more frequently observed species; and  $q = 2$  ( ${}^2D$ ) is Simpson diversity, which can be interpreted as the effective number of dominant species (Chao et al., 2014). We calculated species richness ( ${}^0D$ ) for the entire elevational gradient, although Shannon diversity ( ${}^1D$ ) and Simpson diversity ( ${}^2D$ ) were only analysed from 0 m to 2,500 m due to the low number of species occurring at the two uppermost elevations. We calculated species accumulation curves for each FUI within each elevation using sample-size-based rarefaction and extrapolation (Chao et al., 2014). We used the iNeXT package (Hsieh, Ma, & Chao, 2016) for estimating plot-level diversity and fitting species accumulation curves.

### 2.3.2 | Effect of forest-use intensity on vascular epiphyte diversity across elevation

To test how species diversity and the effects of FUI varied along the elevational gradient, we fitted separate nested analyses of variance for species richness, Shannon and Simpson diversities using the function *aov*, where elevation and FUI nested in elevation were the main factors. We then used Tukey's honest significant differences post hoc test to evaluate differences among FUI levels within each elevation with function *glht* in the R package 'multcomp' (Hothorn, Bretz, & Westfall, 2008). To meet the assumption of normality, all diversity indices were natural logarithm-transformed.

### 2.3.3 | Effect of forest-use intensity and elevation on vascular epiphyte beta diversity

To investigate how species composition varies among FUI levels and along the elevational gradient, we calculated beta diversity using the Sørensen index ( $\beta$ SOR) and partitioned it into its turnover component ( $\beta$ SIM), which indicates that species of a specific site are replaced by other species and its nestedness component ( $\beta$ SNE), which describes a species assemblage of a site as a subset of species of another site, reflecting species loss (Baselga, 2010). In this framework,

$\beta$ SOR =  $\beta$ SNE +  $\beta$ SIM (Baselga & Orme, 2012). We partitioned beta diversity and its components using the function *beta.sample* in the R package 'betapart' (Baselga & Orme, 2012) in two ways: (a) among FUI levels at each elevation and ii) along the elevational gradient for each level of FUI using 1,000 randomly sampled subsets of 5 and 13 plots, respectively. We then calculated mean and 95% confidence intervals to compare beta diversity and its components across elevations and FUI levels. All analyses were performed using R version 3.4 (R Core Team, 2018) with the packages 'vegan' (Oksanen et al., 2016), 'car' (Fox & Weisberg, 2011), 'ggplot2' (Wickham, 2016), 'nlme' (Pinheiro, Bates, DebRoy, & Sarkar, ), 'plyr' (Wickham, 2011), 'ecodist' (Goslee & Urban, 2007), 'MASS' (Venables & Ripley, 2002), 'iNeXT' (Hsieh et al., 2016) and 'betapart' (Baselga & Orme, 2012).

## 3 | RESULTS

Across our 120 study plots, we recorded a total of 271 species of vascular epiphytes belonging to 92 genera and 23 families. The most species-rich families were Orchidaceae (82 species), Polypodiaceae (50), Bromeliaceae (41), Piperaceae (20), Cactaceae (14) and Araceae (12). We found the highest number of species at intermediate elevations (93 species, 1,500 m). We recorded only 17 species at the lowermost elevation and only two species at the uppermost elevation. Identification to species level was possible for 72% of records, while another 26% were identified to genus level, and 1% to family level (for a complete species list, see Appendix S1: Table S1.1).

### 3.1 | Species diversity

Overall, species accumulation curves showed that the highest species richness ( ${}^0D$ ) per FUI ( $n = 5$  plots) was found in OG for sites at 0 m, 1,000 m, 1,500 m and 2,000 m elevation and in DF at 500 m and 2,500 m, whereas SF consistently ranked lowest (Figure 3). Accumulation curves revealed differences in species richness between FUI for three sites, as 95% confidence intervals were not overlapping at 500 m, 1,000 m, and 1,500 m between OG and SF. At the lowermost and two uppermost sites, as well as at 2,000 m and 2,500 m, the rarefaction and extrapolated curves indicated no differences among FUI (Figure 3). Species accumulation curves approached saturation for all sites with the exception of those at 1,500 m and 2,000 m, suggesting that additional sampling at these locations is likely to result in finding more species. Species accumulation curves for Shannon diversity ( ${}^1D$ ) (Appendix S2: Figure S2.1) and Simpson diversity ( ${}^2D$ ) (Appendix S2: Figure S2.2) showed similar patterns, with higher diversity in OG at 0 m, 1,000 m, 1,500 m, 2,000 m and 2,500 m and in DF at 500 m.

### 3.2 | Effect of forest-use intensity on vascular epiphyte diversity across elevation

Plot-level epiphyte species richness ( ${}^0D$ ) varied significantly among elevations ( $F_{7,96} = 73.2$ ,  $p$ -value:  $<.001$ ) and among FUI levels along the elevational gradient ( $F_{16,96} = 2.52$ ,  $p$ -value:  $<.001$ ) (Figure 4).

Shannon and Simpson diversity also varied significantly with elevation (Appendix S3: Table S3.1). Multiple comparisons among FUI and elevation revealed significant differences between OG and SF at 500 m, 1,000 m, 1,500 m and 2,500 m, between OG and DF at 1,500 m ( $p$ -value < .01), between DF and SF at 500 m ( $p$ -value < .1) and between DF and SF at 2,500 m ( $p$ -value < .10, Appendix S3: Table S3.2). Forest-use intensity levels showed similar results, with epiphyte species richness being almost consistent with a mid-elevation peak. Similar patterns were observed for Shannon and Simpson diversity (Appendix S4: Figures S4.1 and S4.2). Species richness was lowest in SF across all study sites. However, at 0 m, 2,000 m, 3,000 m and 3,500 m, we observed no significant differences in species richness within FUI. Similarly, we found no differences in Shannon and Simpson diversities at 0 m and 2,000 m within FUI.

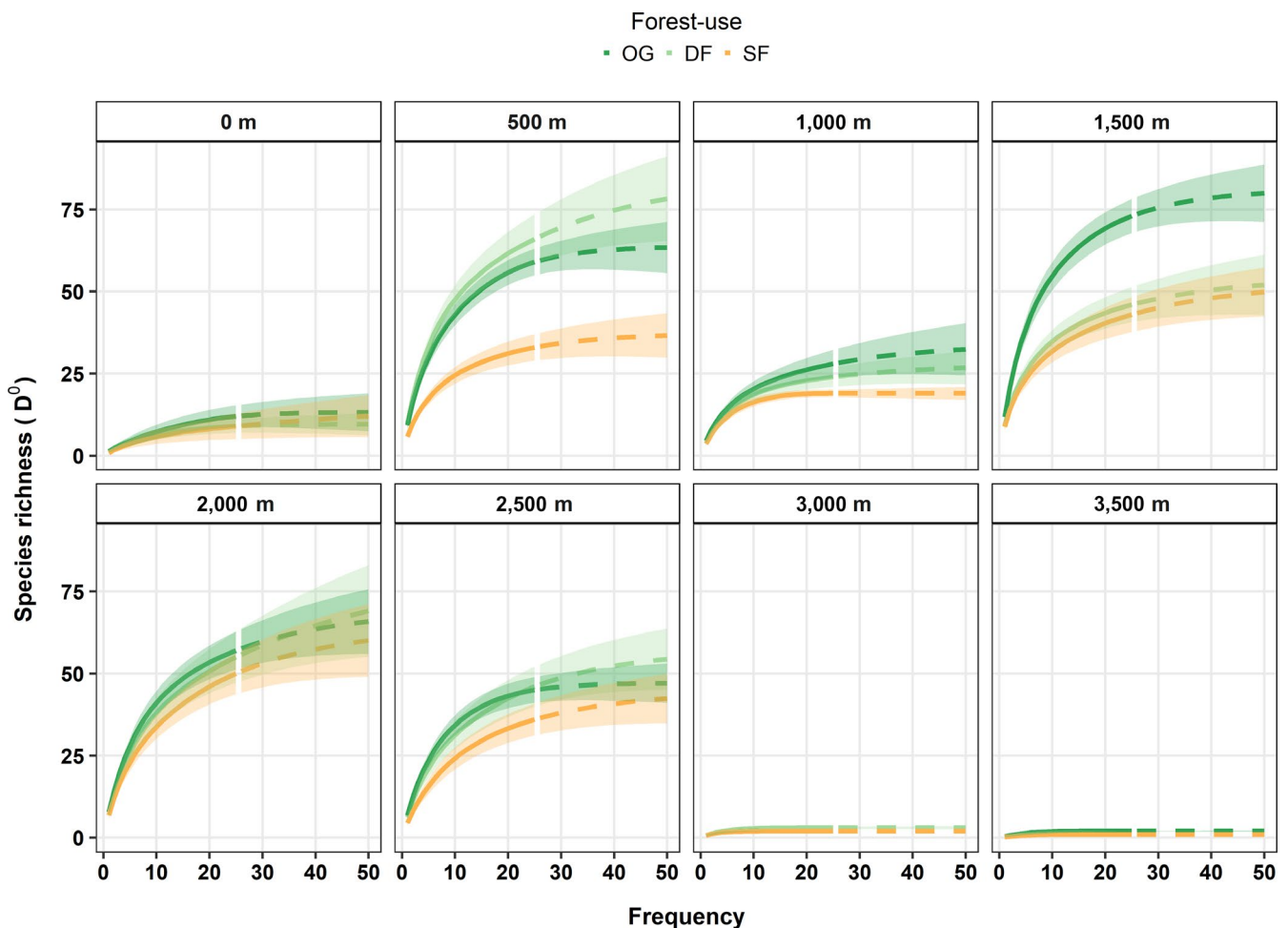
### 3.3 | Effect of forest-use intensity and elevation on vascular epiphyte beta diversity

Across all elevations, beta diversity ( $\beta$ SOR) was dominated by turnover ( $\beta$ SIM) along the forest-use intensity gradient, while nestedness

( $\beta$ SNE) played only a minor role (Figure 5). In general, we found a decrease in  $\beta$ SOR with increasing elevation.  $\beta$ SIM was significantly greater than  $\beta$ SNE across FUI levels, except at 3,500 m where  $\beta$ SNE was higher. Nevertheless, our results show that  $\beta$ SOR (i.e. spatial variation among FUI levels) did not vary with elevation, except for the uppermost elevation (3,500 m, Figure 5). Within each FUI level, we found that beta diversity along the elevational gradient was similar; that is, 95% confidence intervals did overlap (Figure 6). Similarly, beta diversity was dominated by the turnover component (BSIM) along the elevational gradient for each FUI.

## 4 | DISCUSSION

This is the first study to investigate the effect of forest-use intensity on vascular epiphyte diversity and composition along a 3,500-m elevational gradient. We found that the interactive effects of elevation and forest-use intensity strongly impacted local-scale patterns of vascular epiphyte diversity. In parallel, the spatial turnover in species composition among forest-use intensity levels was similar at most



**FIGURE 3** Incidence-based species accumulation curves for species richness of vascular epiphytes, showing rarefaction (solid lines) and extrapolated (dashed lines) curves for species richness Hill numbers ( $^0D$ ),  $n = 5$  plots per forest-use intensity across the eight study sites. Confidence intervals 95% (shaded areas). Abbreviations: old-growth forest (OG; dark green), degraded forest (DF; light green) and secondary forest (SF; orange). See Appendix S3: Figures S3.1 and S3.2 for Shannon ( $^1D$ ) and Simpson ( $^2D$ ) diversities

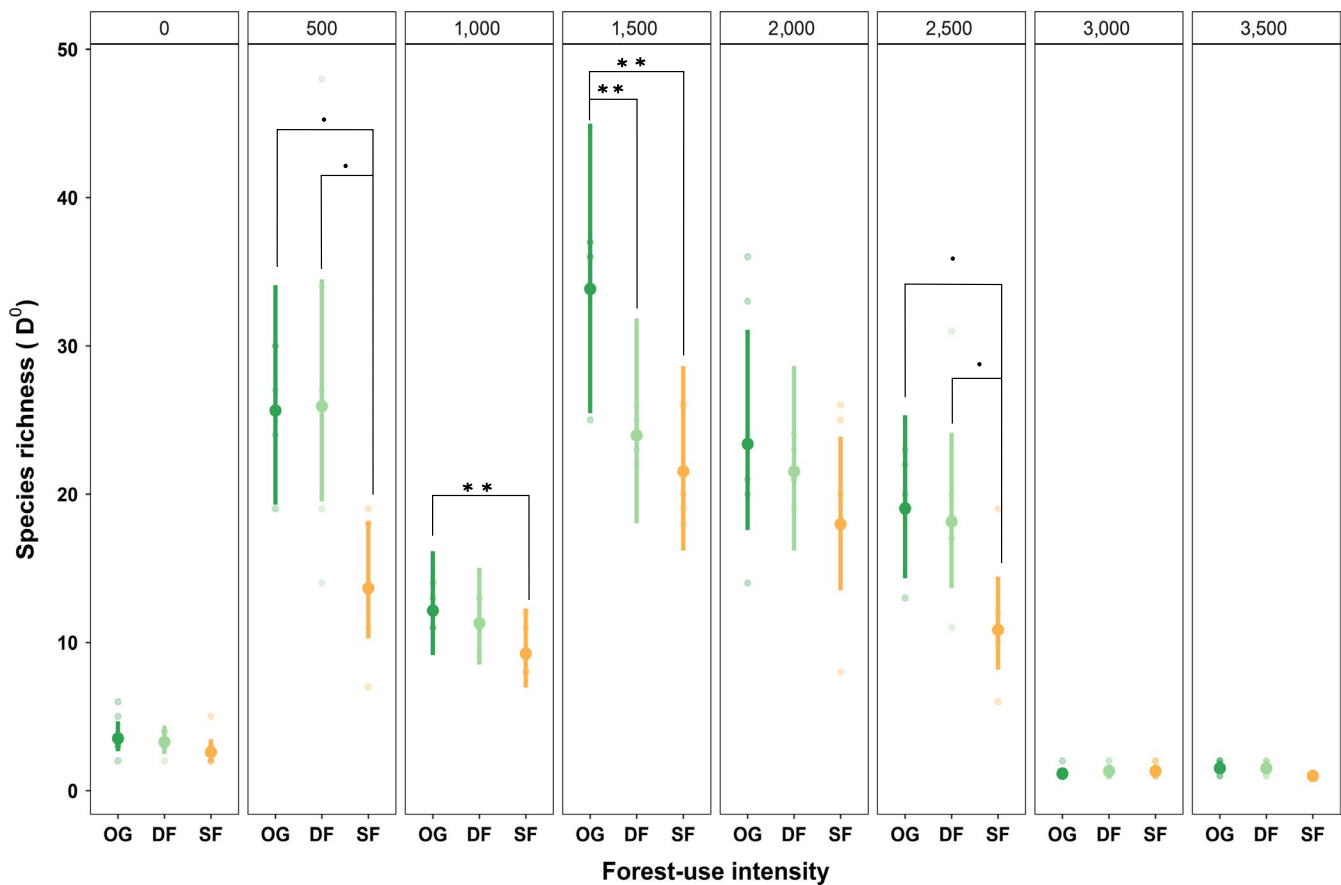
elevational belts and—with the exception of the highest elevations—was dominated by the turnover component of beta diversity.

#### 4.1 | Elevational patterns in vascular epiphyte diversity

In line with our first hypothesis, we found that species richness of vascular epiphytes along the Cofre de Perote transect peaked in humid montane forests at mid-elevations and monotonically decreased from 1,500 m towards the upper limit of the elevational gradient. This observation is consistent with previous studies on elevational patterns in epiphytes (Cardelús et al., 2006; Kessler, Kluge, Hemp, & Ohlemüller, 2011; Kluge et al., 2006; Krömer et al., 2005; Wolf & Flamenco, 2003). Unexpectedly, species richness showed a bimodal pattern with a second peak of species richness occurring in tropical oak forests at 500 m. It is unclear whether this deviation from the expected hump-shaped pattern (McCain & Grytnes, 2010) is due to an unusually high diversity found at 500 m, which was on average comparable to diversity at 1,500 m, or an unusually low diversity of vascular epiphytes at the 1,000-m site. Interestingly, the low gamma richness of epiphyte communities at

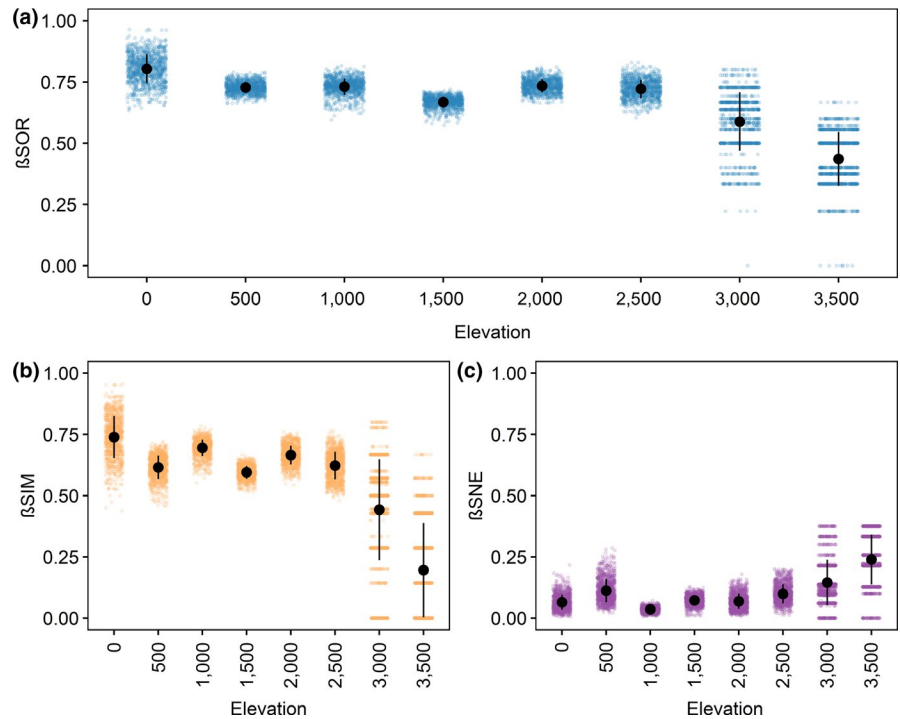
1,000 m (40 species) compared to 500 m (89) mirrors results of previous studies on terrestrial herbaceous angiosperms (Gómez-Díaz et al., 2017) and ferns and lycophytes (Carvajal-Hernández & Krömer, 2015) in the same study area. The lower species richness at 1,000 m might also be not related to lower rainfall at this elevation (Carvajal-Hernández & Krömer, 2015). Few species occurred at the lowest end of the elevational gradient, which we attribute to the pronounced dry seasons, deciduous host trees, high mean annual temperatures and low mean annual precipitation (Gentry & Dodson, 1987; Kreft, Köster, Küper, Nieder, & Barthlott, 2004). Furthermore, this site is located close to the Gulf of Mexico, where the studied forests grow on sandy soils and are exposed to strong winds and high salinity (García-Franco, 1996).

Above 2,000 m, epiphyte diversity declined with elevation in all forest-use intensities, most likely reflecting changing climatic conditions. A potential explanation for declines of epiphyte diversity at higher elevations is low temperatures and frequent frost events above 3,000 m ( $-3^{\circ}\text{C}$  absolute minimum temperature; Carvajal-Hernández, unpublished data; Bhattarai et al., 2004; Krömer et al., 2005). Additionally, it is important to note that the only three species found at both uppermost elevations were ferns of the Polypodiaceae family. Interestingly,

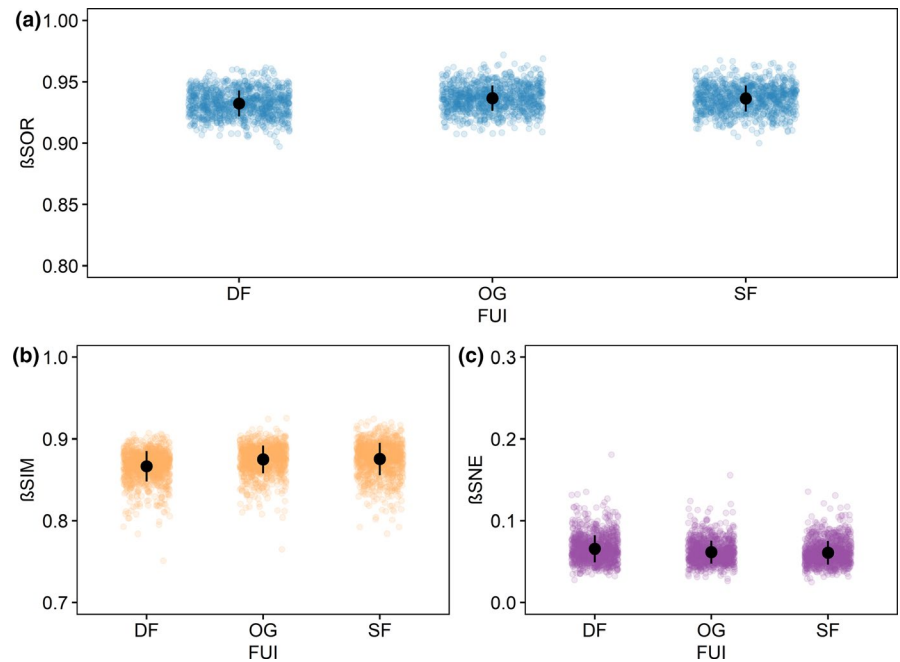


**FIGURE 4** Variation in species richness ( $D^0$ ) of vascular epiphytes across different levels of forest-use intensity along an elevational gradient. 95% confidence intervals shown with colour bars. We tested multiple comparisons among forest-use intensity types ( $n = 5$  plots per forest-use intensity across the eight study sites), which revealed significant differences between OG and SF at 500 m, ( $p$ -value  $< .1$ , indicated as '), at 1,000 m ( $p$ -value  $< .05$ , indicated as '\*\*'), at 1,500 m ( $p$ -value  $< .01$ , indicated as '\*\*\*') and 2,500 m ( $p$ -value  $< .1$ , '); between OG and DF at 1,500 m ( $p$ -value  $< .01$ , '\*\*\*'); and between DF and SF at 500 m ( $p$ -value  $< .1$ , ') and at 2,500 m ( $p$ -value  $< 0.1$ , ', Appendix S3: Table S3.2)

**FIGURE 5** Beta diversity across the forest-use intensity gradient within each elevational belt. Beta diversity is based on the Sørensen index (a;  $\beta$ SOR) and partitioned into both its turnover component (b;  $\beta$ SIM) reflecting species replacement and nestedness component (c;  $\beta$ SNE) reflecting species loss of vascular epiphytes. Each black point represents average beta diversity, which was derived from 1,000 randomly sampled subsets of five plots within each elevation belt across forest-use intensity gradient. Bars are 95% confidence intervals



**FIGURE 6** Beta diversity across elevations within each forest-use intensity type. Beta diversity is based on the Sørensen index (a;  $\beta$ SOR) and partitioned into its turnover component (b;  $\beta$ SIM) reflecting species replacement and nestedness component (c;  $\beta$ SNE) reflecting species loss of vascular epiphytes. Each black point represents average beta diversity based on 1,000 randomly sampled subsets of 13 plots within each forest-use intensity across the elevational gradient. Bars are 95% confidence intervals



Polypodiaceae species were also reported as the highest growing epiphytes above 4,000 m in the Peruvian Andes (Sylvester, Sylvester, & Kessler, 2014) and *Polypodium vulgare* is also the epiphyte species with the northernmost and highest occurrences in Europe, where it is able to survive prolonged periods of frost (Zotz, 2005). Because all these regions are comparatively humid, we tentatively suggest that frost is a main constraining factor at upper elevations. Besides the effect of harsh climatic condition, an alternative factor might be that conifers of the genera *Pinus* and *Abies* are poor epiphyte hosts. Whereas there is no information about the quality of *Abies* as hosts, pines have been considered as poor epiphyte hosts, not only because of phenolic and

resinous substances (Hietz & Hietz-Seifert, 1995; Wolf, 2005) but also because of low water-holding capacities of their bark (Callaway, Reinhart, Moore, Moore, & Pennings, 2002). Additionally, the monopodial growth and lack of large horizontal branches of some conifers might be a constraining factor limiting epiphyte abundance and diversity.

#### 4.2 | Effect of forest-use intensity on vascular epiphyte diversity across elevation

Contrary to our second hypothesis, we did not observe a consistent decrease in species richness with increasing forest-use intensity. We



expected that vascular epiphytes would be particularly affected by the conversion of intact forest into other land-use types, mainly because of the loss of suitable host trees that provide a complex mosaic of microhabitats (Benzing, 1995; Hietz-Seifert, Hietz, & Guevara, 1996). This has been shown previously in studies demonstrating that epiphyte diversity decreases with increasing levels of disturbance in montane areas (Barthlott et al., 2001; Köster et al., 2009; Krömer & Gradstein, 2003; Nöske et al., 2008; Wolf, 2005).

We present evidence that this pattern does not always hold. Species diversity may even be slightly higher in more disturbed areas, such as DF occurring at 500 m, a pattern which also has been reported from Indonesia (Böhnert et al., 2016). However, species richness was consistently lowest in SF across all elevations and differed significantly from OG at half of the sites (Figure 4). The largest differences in species diversity between OG, DF and SF were observed at 1,500 m (Figure 4). Our results are in line with Carvajal-Hernández, Krömer, López-Acosta, Gómez-Díaz, and Kessler (2017), who found a significant reduction in fern species richness in disturbed and secondary forests compared to the intact forest, which the authors related to changes in forest structure and microclimate. Moreover, Krömer et al. (2014) found that a disturbed forest at this elevation had reduced species richness of epiphytes due to harvesting activities of epiphytes (mainly orchids) that are sold as ornamental plants in local markets (Flores-Palacios & Valencia-Díaz, 2007; Toledo-Aceves, Hernández-Apolinar, & Valverde, 2014).

At the two uppermost elevations, we did not find differences in species diversity among FUI levels. This likely reflects the low local species richness where the few fern species present are physiologically pre-adapted to tolerate environmental conditions at high elevations (Hietz, 2010; Stuart, 1968), which might also be an advantage in degraded and secondary forests. At the lowest elevation, we did not observe differences in species diversity among FUI levels either, again reflecting the low overall species richness, which may be attributable to the physiological and morphological pre-adaptations of drought-tolerant species to cope with changes in forest structure (Barthlott et al., 2001). While OG forests had the highest species richness in most of our study sites (except 500 m and 2,500 m), DF and SF also showed comparable levels of species richness at most elevations (Figure 4), highlighting the potential of degraded and secondary forests to maintain, to some extent, the epiphyte diversity in tropical forests (Böhnert et al., 2016; Chazdon, Peres, et al., 2009). However, species with specific habitat requirements, such as shade- and humidity-adapted understory orchids and ferns, might not be able to persist in highly disturbed forests (Krömer et al., 2014) and can only be protected in old-growth forests. Furthermore, other forest- or land-use types that maintain isolated trees or live fences where epiphytes can persist should be taken into account when developing conservation strategies (Einzmann & Zotz, 2016; Köster et al., 2009).

#### 4.3 | Effect of forest-use intensity and elevation on vascular epiphyte beta diversity

Our results show that the magnitude of spatial turnover of vascular epiphyte community composition across FUI levels was similar

within most elevations and that it was usually dominated by the turnover component of beta diversity. This suggests that similar ecological mechanisms, such as niche partitioning, operate along the entire elevational gradient and likely determine shifts in community composition (Soininen, Heino, & Wang, 2018). Our results agree with those of previous studies, which have reported changes in the composition of vascular epiphytes across land-use or habitat types, for example preserved forests and forest fragments or isolated trees in pastures (Barthlott et al., 2001; Benavides, Wolf, & Duivenvoorden, 2006; Flores-Palacios & García-Franco, 2008; Hietz-Seifert et al., 1996; Larrea & Werner, 2010; Werner et al., 2005; Wolf, 2005).

Along the elevational gradient, we found no difference in beta diversity among forest-use intensity levels (Figure 6). This suggests that even when controlling for differences in forest-use intensity, species composition in vascular epiphyte communities is strongly regulated by the changes in environmental conditions that occur along the elevational gradient. Moreover, the high relative importance of the turnover component illustrates the high degree of habitat specialization of epiphytes within each forest-use intensity level. Thus, our analysis reveals that similar ecological processes, for example niche partitioning, likely operate along both forest-use intensity (Figure 5) and elevational gradients (Figure 6) via their influence on microclimate.

## 5 | CONCLUSIONS

We found that interactive effects of elevation and forest-use intensity strongly influence the spatial patterns of vascular epiphyte diversity in this tropical mountainous region. Our results also show that the impact of forest-use intensity on epiphyte diversity is not consistently negative, suggesting that tropical landscapes with degraded and secondary forests can maintain high levels of epiphyte diversity. Degraded and—to a lesser extent—secondary forests may host a considerable level of epiphytic biodiversity and therefore may act as reservoirs for conservation and restoration. The differences between forest-use intensity levels only emerged at the scale of gamma diversity, calling for a landscape-level perspective to understand the effects of land-use change on tropical biodiversity. Consequently, conservation and restoration initiatives should integrate such a perspective by conserving heterogeneity within landscapes, rather than relying uniquely on the protection of old-growth forest fragments.

## ACKNOWLEDGEMENTS

We thank A. Smith, A. Espejo-Serna, A. R. López-Ferrari, G. Mathieu, M. Cházaro-Bazáñez and P. Carrillo-Reyes for the taxa determination. We thank J. Veà, A. Bautista, M. Juárez-Fragoso, C. Carvajal, J. Gómez, D. Vergara, N. Velázquez, F. Calixto-Benites, M. Hernández, J. Ramírez and S. Guzmán for their help during fieldwork; P. Weigelt for help with data management; N. Guerrero for statistical support; and R. Castro for help with herbarium specimens. We appreciate the

opportunity to use the facilities from the Centro de Investigaciones Tropicales, Universidad Veracruzana, Xalapa, Mexico. The German Academic Exchange Service (DAAD) provided a PhD scholarship (No. 91570360) to V. Guzmán-Jacob.

## DATA AVAILABILITY STATEMENT

Data underpinning the analyses are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c5d5h3b>


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#### BIOSKETCH

**Valeria Guzmán-Jacob** is interested in the diversity, ecology and conservation of tropical plants, with an emphasis on biodiversity patterns of vascular epiphytes and tropical forests. This paper is part of her PhD work at the University of Göttingen.

Author contributions: V.G.J, H.K and T.K conceived the main idea with input from G.Z; V.G.J collected the data; and V.G.J analysed the data with support from D.C and H.K. The manuscript was written by V.G.J, with input of A.T and M.L.M.G. All authors made substantial contributions to the interpretation of results and the editing of the manuscript.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**How to cite this article:** Guzmán-Jacob V, Zotz G, Craven D, et al. Effects of forest-use intensity on vascular epiphyte diversity along an elevational gradient. *Divers Distrib*. 2020;26:4–15. <https://doi.org/10.1111/ddi.12992>