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Research article

Significance of remnant cloud forest fragments as reservoirs of tree and epiphytic bromeliad diversity

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Abstract

Tropical Montane Cloud Forests (TMCF) support exceptional concentrations of biodiversity but are severely threatened by deforestation. In Mexico, 60% of TMCF tree species has been reported as threatened, and the epiphytic plants characteristic of these forests are particularly vulnerable to disturbance and climate change. We evaluated the role of remnant TMCF fragments as reservoirs of tree and epiphytic bromeliad biodiversity in southeastern Mexico. In four cloud forest fragments of varying size (1.2, 4.1, 6.6 and 9.8 ha), we recorded all trees $\geq$ 10 cm dbh in six 20 x 10 m plots and sampled eight trees at each site to measure bromeliad diversity. The assessment revealed that even very small forest fragments can host significant tree and epiphytic bromeliad diversity. In total, 45 tree and 18 bromeliad species were recorded among all the sites. These forest fragments are an important reservoir of both endemic tree species (seven species) and those with conservation status (nine tree species and one bromeliad species). Important variation in tree and bromeliad composition was found among fragments. This high heterogeneity among forest sites means that maintenance of even small fragments can play a strategic role in the conservation of biodiversity in the severely transformed landscape of the region. Such maintenance merits full consideration in the design of forest management policies and TMCF restoration initiatives.

Key words: Tropical montane cloud forest, biodiversity conservation, deforestation, Mexico.

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Introduction

Tropical Montane Cloud Forests (TMCF) are a global conservation priority because they host exceptional concentrations of biodiversity and are severely threatened by deforestation and global climate change [1-3]. Due to their naturally limited distribution in mountain zones within a relatively narrow cloud belt, TMCF distribution is often analogous to an archipelago, with deforestation acting to further isolate remaining TMCF sites. As a result of the severe reduction in TMCF area, the remnant fragments have become essential to the conservation of important biodiversity [4].

The tree community defines the forest structure and plays a central role in the ecological function and resilience of TMCF [5]. Unfortunately, 60% of TMCF tree species in Mexico has been reported as vulnerable, threatened, endangered, or even extinct [5]. Epiphytes are a defining characteristic of TMCF, representing up to 50% of its plant species [6-8]. Bromeliads account for an important proportion of all the vascular epiphytes present in cloud forests [9, 10]. Deforestation, habitat degradation and climate change threaten the maintenance of epiphytic plants in these ecosystems [6, 10-13]. Consequently, various epiphytic bromeliad species are listed as threatened and have become locally rare in areas of Mexico [14-16]. The diversity of trees and epiphytic bromeliads may therefore be used as an indicator of TMCF conservation status.

TMCF deforestation and fragmentation threaten the maintenance of biodiversity. With reduced fragment area and associated increases in isolation and edge effects, a decline in epiphytic bromeliad and tree biodiversity can be expected [17-19]. Since habitat loss causes extinction of populations, the number of individuals of a given species that the landscape can support must be a positive function of the amount of available habitat. However, this relationship may not be proportional [20], perhaps due to a threshold in available habitat below which a population cannot be self-sustaining [20]. Nevertheless, small forest fragments can support diverse communities of native plants [21], and their conservation can be of particular importance in highly deforested landscapes [22, 23]. In this study, we assessed the role of remnant TMCF fragments in supporting tree and epiphytic bromeliad diversity. Because bromeliad species richness in Mexico peaks in drier lower montane forests rather than in cloud forests [24], this study was carried out in the TMCF belt corresponding to the lower montane forest [25], where bromeliads may be indicator species of this type of forest. We hypothesised that even small fragments can support an important diversity of epiphytic bromeliads and trees within a severely transformed landscape, such as that of Central Veracruz, Mexico.

Methods

Study Area

The study was conducted in the TMCF region of Central Veracruz, Mexico, in the mid-watershed of the river Pixquiac (Fig. 1). The studied fragments correspond to TMCF [18, 25], equivalent to “bosque mesófilo de montaña” [26]. The climate is mild and humid throughout the year; total annual precipitation varies between 1,350 and 2,200 mm, and the mean annual temperature is between 12 and 18 °C [18]. Three seasons are recognized: a relatively dry cool season (October to March), a dry warm season (April and May), and a wet warm season (June to September) [27]. In this region, four forest fragments located between 1,460-1,660 m asl were selected based on patch size and the owners’ commitment to a bromeliad management project (Table 1). The fragments were located an average of 1.92 km apart, with the greatest distance between sites 1 and 2 (2.34 km) and the shortest distance between sites 1 and 4 (0.45 km). The forest fragments ranged from 1.2 to 9.8 ha in area and were immersed within a matrix of forest, pasturelands, crops (mainly maize), and secondary vegetation in various degrees of recovery. Within the study area, the TMCF has been subjected to firewood collection, illegal selective logging, livestock free-grazing within the forest, and harvesting of epiphytes as non-timber forest products (NTFP) for ornamental and ceremonial purposes [28]. The impacts of these activities on forest conservation status are poorly understood. Epiphytic bromeliads are locally known as “tenchos”. Harvesting of epiphytes had not occurred in the selected fragments; however, unplanned and illegal selective tree logging has taken place in all the sites for the last 80 years [28]. Cattle have been grazed in the past within parts of the forest fragments in all the sites, producing an impoverished understory.

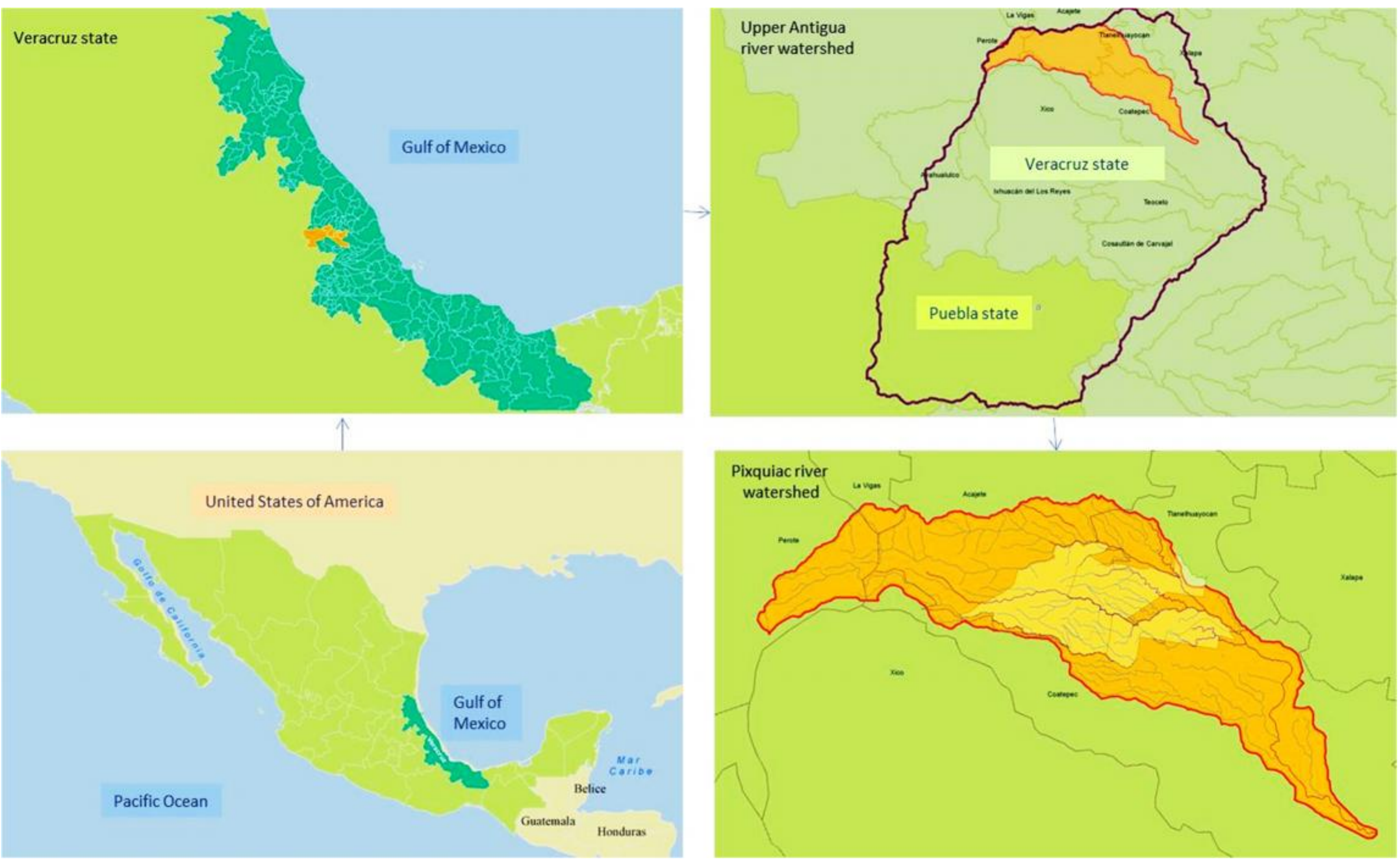

Fig. 1 Location of the watershed of river Pixquiac, Veracruz, Mexico.

Six 10 x 20 m plots were established per site. In each plot, trees ≥ 10 cm diameter at 1.3 m (dbh) were measured and identified. Bromeliad richness and abundance were determined on eight trees at each site. *Liquidambar styraciflua* and *Quercus* spp. canopy trees were selected based on accessibility and non-overlapping crowns. Each tree was climbed with single rope techniques [29]. Tree and bromeliad samples were collected and voucher specimens were deposited at the XAL herbarium. Specimens that could not be identified to species level were identified to genus.

Data analysis

In each site, we calculated the importance value index, richness, Shannon-Wiener diversity index (H´), basal area, density and mean dbh for the trees, and species richness and rosette abundance per tree for the bromeliads.

Tree dbh, basal area (BA), density and bromeliad abundance (number of rosettes per tree) were compared among sites using a generalized linear model GLM [30]. Since numbers of rosettes are counts, a Poisson distribution was assumed and a log link function was used. To compare bromeliad abundance among forest sites, tree dbh was included as a covariate to correct for differences associated with tree size. Analyses were performed with MINITAB 16 (Minitab Inc. 2010) and SPSS 20 (IBM Corp. 2011).

To facilitate interpretation of the relationship between bromeliad species and abundance and their host trees, a canonical correspondence analysis (CCA) with the program CANOCO, version 4.5 [31] was conducted on bromeliad abundance for each tree and a set of explanatory variables (BA, no. of rosettes and richness). We used forward selection for ranking the importance of explanatory variables, and their statistical significance was judged by a Monte Carlo permutation test [31].

The Shannon-Wiener diversity index (H´) was calculated in order to estimate tree diversity at each site. A randomization test, based on re-sampling with 10,000 random permutations, was used to test the significance of the difference in indices among sites [32]. In addition, the Jaccard index was calculated in order to elucidate the similarity among forest sites. Species, Diversity and Richness Software V4.0 was used for these analyses.

The importance value Index (IVI) of the tree species in each site was calculated by adding the relative number of individuals, relative BA, and relative frequency [33]. Relative values were calculated by dividing the observed value of each species by the total of species.

Results

Cloud forest fragment structure and composition

A total of 45 tree species was recorded in the four forest sites. Of these, 34 taxa were identified to species, 10 to genus, and one was recorded as unknown. Richness varied between 14 and 21 species per site and H' was higher at sites 1 and 2 than at sites 3 and 4 (Table 1). Site 1, the smallest fragment, displayed the highest species richness and diversity. According to IV, the dominant tree species were *Clethra macrophylla*, *Liquidambar styraciflua*, *Quercus cortesii*, *Q. delgadoana* and *Q. lancifolia* (Table 2). *Quercus* spp. represented a lower proportion of the total basal area in site 1 (19%) and site 2 (14%) than at site 3 (59%) and site 4 (57%). The Jaccard index indicated low similarity in species composition between pairs of sites. Site 2 was more similar to other sites, followed by sites 3 and 4 (Fig. 2).

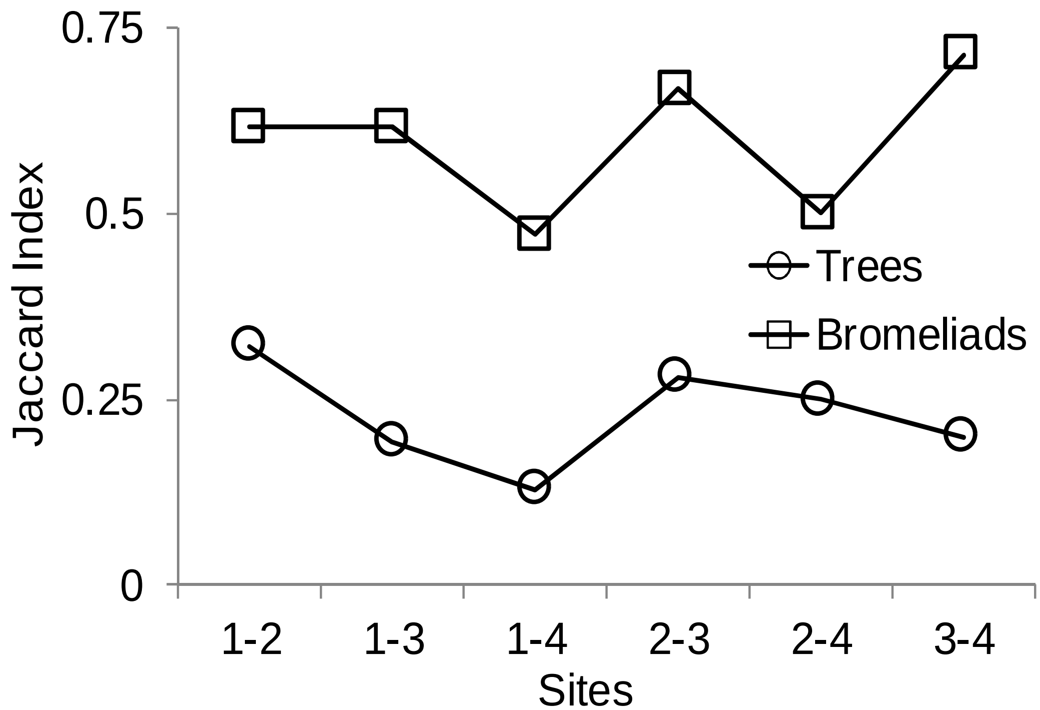

Fig. 2 Estimated similarity between pairs of study sites, according to the Jaccard index, in TMCF, central Veracruz, Mexico. 0 indicates that composition is different and 1 indicates complete similarity.

Forest structure was similar among forest fragments; mean diameter and basal area were statistically similar among sites, but tree density was lower at site 2 than at the other sites (Table 1). Diameter classes, considering all tree species together, followed an inverted J-shape distribution in sites 2, 3, and 4; in site 1, the smallest size category (10-20 cm) was not well represented (Fig. 3). The contribution of the smallest size category in sites 2, 3, and 4 ranged from 43 to 49 % (considering all species together), but was below 35% at site 1. Tree species with $\geq$ 70 cm diameter were recorded in all the study sites. These included species such as *Clethra macrophylla*, *Quercus cortesii*, *Q. delgadoana*, *Q. lancifolia, Q. sartorii*, and *Saurauia pedunculata*.

Epiphytic bromeliads

In total, 18 species of epiphytic bromeliads were recorded. Richness varied from 9 to 12 species (Table 1). Comparison of the Shannon-Wiener index showed that all sites presented significantly different bromeliad diversity values. Site 4 hosted the highest diversity and Site 3 the lowest (Table 1). Overall, the Jaccard index was high for the bromeliad communities in the four sites (Fig. 2). The abundance of *Tillandsia butzii* (6.9%), *T. kirchhoffiana* (20.7%), *T. multicaulis* (51.3 %) and *T. punctulata* (16.3%) accounted for 95.2% of total bromeliad abundance throughout all the sites (Table 3). Bromeliad abundance differed significantly among sites (Wald chi-square = 4540.35, DF = 3, P < 0.0001), and tree diameter was significant as a covariate (Wald chi-square = 356.74, DF = 1, P

< 0.001): bromeliad abundance at site 4 was seven to eight times higher than at the other sites (Table 1).

Table 1. Characteristics of the four study sites in the tropical montane cloud forest region of central Veracruz, Mexico. A. Study site geographical information. B. Tree vegetation variables are species richness, Shannon diversity index (H'), mean diameter (cm), density (trees ha^{-1}), and basal area (m^2 ha^{-1}) of trees $\geq$ 10 cm dbh. C. Bromeliad variables are species richness, H' and rosettes per tree. Values in parentheses denote the standard error. Different letters denote significant differences among forest sites ($P < 0.05$). Connected refers to the status of a fragment that is connected or attached to continuous forest.

	Site 1	Site 2	Site 3	Site 4
A. Site				
Area (ha)	1.2	4.1	6.6	9.8
Connected	No	Yes	Yes	Yes
Latitude N	19° 30' 26"	19° 31' 03"	19° 32' 16"	19° 30' 57"
Longitude W	96° 59' 09"	97° 00' 25"	96° 59' 57"	96° 59' 58"
Elevation (m asl)	1460	1660	1660	1580
B. Tree vegetation				
Richness	21	16	16	14
H'	2.66 [a]	2.60 [a]	1.93 [b]	2.18 [b]
Diameter	26.7 (1.5, N = 64)	29.9 (2.7, N = 46)	27.6 (1.9, N = 91)	30.8 (2.6, N= 75)
Density	533 (104)[a]	383.3 (72.6)[b]	758.3 (98.7)[a]	625 (64.2)[a]
Basal area	35.7 (11.3)	37.1 (12)	65.2 (9.2)	71.9 (21)
C. Bromeliad				
Richness	9	10	10	12
H'	1.22 [a]	1.31 [b]	0.70 [c]	1.4 [d]
Rosettes per tree	312 (87)[a]	385 (61)[a]	368 (56)[a]	2636 (367)[b]

The CCA was carried out for 32 host trees and 18 species of bromeliads with three explanatory variables (number of rosettes per tree, bromeliad richness per tree, and tree basal area). Axis 1 (eigenvalue = 0.165) and axis 2 (eigenvalue = 0.021) described 81% and 10% of the species-environment relationship (Monte Carlo test of first axis $F = 6.179$, $P = 0.02$; test of all canonical axes $F = 2.663$, $P = 0.016$). The only significant explanatory variable was number of rosettes per tree. Ordination of trees clearly showed a separation between the trees in site 4 and those in the other three sites (Figure 4). In terms of bromeliad composition, site 4 differed from the other sites due to the higher relative abundance of *T. punctulata*, lower relative abundance of *T. multicaulis* and the presence of rarer species such as *T.* aff. *fasciculata, Racinaea ghiesbreghtii*, *T. lucida* and *T. tricolor* (Table 3), whereas *T. belloensis*, *T. gymnobotrya*, *T. heterophylla* and *T. macropetala* were associated with trees in the other sites (Fig. 4).

Table 2. Importance value index (IVI) for the 12 tree species with IVI greater than 5% in any study site. Conservation status is presented following González-Espinosa et al. (2011). E is endangered, V is vulnerable, NT is near threatened, and LC is of least concern.

Tree species	Conservation status	Site 1	Site 2	Site 3	Site 4
Carpinus tropicalis	NT	-	-	6.54	-
Clethra macrophylla	LC	6.61	15.49	13.68	2.15
C. schlechtendalii	LC	4.22	5.31	-	-
Hedyosmum mexicanum	LC	6.74	8.24	1.47	9.49
Liquidambar styraciflua	LC	15.35	17.56	14.43	26.52
Quercus cortesii	NT	-	-	-	19.93
Q. delgadoana	E	-	-	34.77	-
Q. lancifolia	NT	14.49	7.27	6.59	9.65
Q. sartorii	EN	-	3.10	4.38	12.23
Styrax glabrescens	VU	7.01	7.30	1.45	-
Turpinia insignis	EN	10.92	7.39	1.58	-
Saurauia pedunculata	VU	-	9.53	-	-
33 other species		34.66	18.82	15.11	20.04

Discussion

The results show that even very small forest fragments can host significant tree and epiphytic bromeliad diversity. In other studies in the same region, using a greater number of larger forest sites, similar numbers of tree species have been reported [25]. Interestingly, we found more bromeliad species than those reported by Hietz and Hietz-Seifert [34; 13 bromeliad species in 35 trees in one TMCF site] and Krömer et al. [35; 9-12 species in three fragments of TMCF], while Flores-Palacios and García-Franco [36] reported the same number (18) of bromeliad species but in a greater number of habitats (pasture, riparian forest and forest interior) and trees (108). These forests are also important reservoirs of seven endemic tree species and nine with conservation status (IUCN red list [5]). For example, *Quercus delgadoana*, an endemic species classified as endangered, was a dominant species in one site, and *Styrax glabrescens* and *Symplocos limoncillo*, classified as vulnerable, were common in three and two of the study sites, respectively.

The relatively high tree diversity found in the studied fragments could be explained by the increased amount of light near edges and gaps, promoting the establishment of pioneer species [37] such as *Trema micrantha*, *Myrsine coriacea*, *Solanum* spp. and *Eupatorium* spp. Other tree species common in the sites, e.g., *Clethra macrophylla* and *Hedyosmum mexicanum*, are also favored by disturbance [5, 38]. Nevertheless, elements of old growth forest and mature forest in the region [38] such as *Quercus delgadoana*, *Q. sartorii*, *Q. lancifolia, Saurauia pedunculata* and *Turpinia insignis,* were identified within all of the fragments. It is noteworthy that the smallest fragment hosted the greatest tree species richness, including those species considered characteristic of old growth TMCF, demonstrating that an important reservoir of mature forest elements can survive in even very small

TMCF fragments. Furthermore, the high heterogeneity of composition found among fragments means that even small and disturbed fragments can play an important role as reservoirs of TMCF biodiversity within the severely transformed landscape of the region [25, 39].

Table 3. Relative abundance (%) of epiphytic bromeliad species within four fragments of tropical montane cloud forest in central Veracruz, Mexico. *Catopsis* spp. includes *Catopsis sessiliflora* and *C. nutans* and *Tillandsia* spp. includes *Tillandsia* seedlings.

Species	Site 1	Site 2	Site 3	Site 4
Catopsis spp.	1.48	3.54	0.95	0.89
Racinaea ghiesbreghtii	0	0	0.31	0.61
Tillandsia belloensis	0.08	0	0	0
T. butzii	2.17	5.52	7.47	12.64
T. deppeana	0.08	0	0	0
T. aff. *fasciculata*	0	0	0	0.17
T. gymnobotrya	0	0.19	0	0
T. heterophylla	0.72	0.1	0	0
T. juncea	0.84	0.03	0.34	0.61
T. kirchhoffiana	24.54	40.46	3.5	14.14
T. lucida	0	0	0	0.05
T. multicaulis	55.37	39.62	82.29	28.15
T. punctulata	9.14	9.47	4.21	42.41
T. schiedeana	2.57	0.03	0.03	0.23
T. tricolor	0	0	0	0.08
T. macropetala	0	1.04	0.31	0
Tillandsia spp.	3.01	0	0.61	0.02

The trend of lower abundance of *Quercus* spp. in the smaller fragments may indicate regeneration problems, suggesting, as has been found in other montane forests [40, 41], a threshold beyond which the structure of this tree community is altered in areas that are more exposed to disturbance. Muñiz-Castro et al. [38] reported a clear increase in *Quercus* spp. dominance in mature forests in central Veracruz. Selective logging for firewood is very common in TMCF [2], and this practice may have a severe negative impact on tree regeneration by eliminating large seed-source trees, particularly in the case of *Quercus* spp., which are preferred for their wood quality [42]. The reduced number of trees with a dbh > 60 cm in the smallest fragment in particular may contribute to reduced seed production. Increased mortality of seedlings of old-growth trees near the edges [37] could also explain the lower proportion of *Quercus* spp. in the smaller fragments. The local disappearance of certain species could yet occur; habitat destruction and fragmentation can cause time-delayed extinction [43]. In order to provide a more complete diagnostic of the remnant TMCF condition, an evaluation of tree regeneration patterns in the region is necessary.

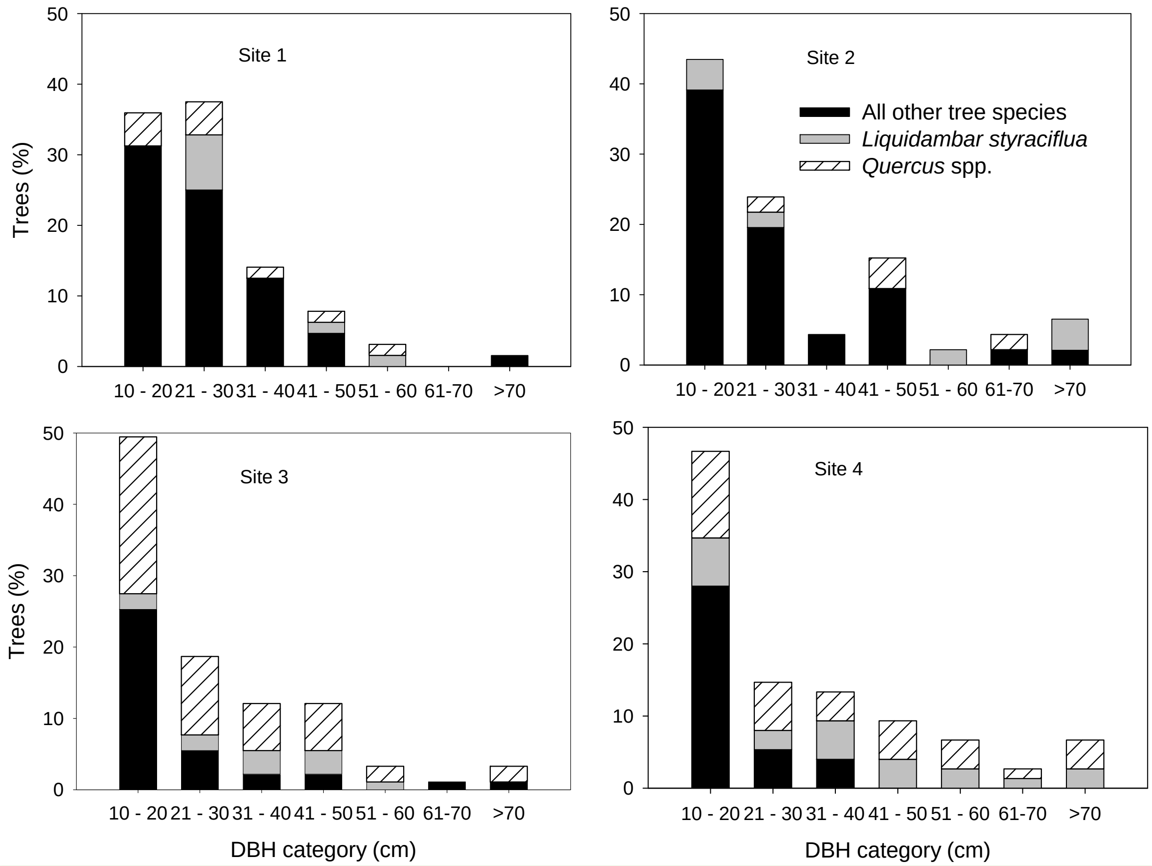

Fig. 3. Percentage of tree according to size category in four tropical montane forest fragments in central Veracruz, Mexico, DBH = diameter at breast height.

Tree and bromeliad diversity did not display similar trends; one site may simultaneously display the lowest bromeliad and tree diversity, while another site displays the highest bromeliad diversity with relatively low tree diversity. This lack of pattern is probably due to the intrinsically high heterogeneity of TMCF [1, 4, 25], as well as to past and present interventions such as selective logging and cattle grazing inside the forest. To improve our understanding of the mechanisms involved in the anthropogenic effects on forest conservation status, we recommend an evaluation that includes a wider range of forest fragment sizes, as well as more details of management history. Factors such as large basal area, which provides a larger surface area for attachment, can increase the number of epiphytic species. Also, larger fragment size may imply fewer edge effects on tree and epiphyte diversity.

Epiphytes in general have been recognized as sensitive indicators of forest disturbance [10, 44, 45]; however, not all groups or even species within the same genus respond equally [8, 35, 39]. Various bromeliad species increase in abundance and contribute greatly to the diversity of disturbed montane forests [10, 11, 46]. Three of the most dominant species at all sites, *T. kirchhoffiana, T.*

punctulata and *T. multicaulis,* have been reported to increase in abundance in disturbed forests, on isolated trees in pasturelands [11, 47], and even in shaded coffee plantations [48]. More drought-tolerant bromeliad species, such as *T. schiedeana* [49, 50] and *T. juncea*, were more abundant in the smallest fragment, reflecting the mesic conditions (T. Toledo-Aceves, unpublished data). Bromeliads are among the most prominent epiphytes in many Neotropical forests, but their diversity and/or abundance decline in some upper TMCF compared to orchids, ferns, and other groups in Mexico [24], while bromeliad diversity can even peak in the upper montane forests of other regions [51, 52]. The evaluation of other groups of epiphytes and TMCF at higher altitudes would therefore provide a more complete representation of the cloud forest condition.

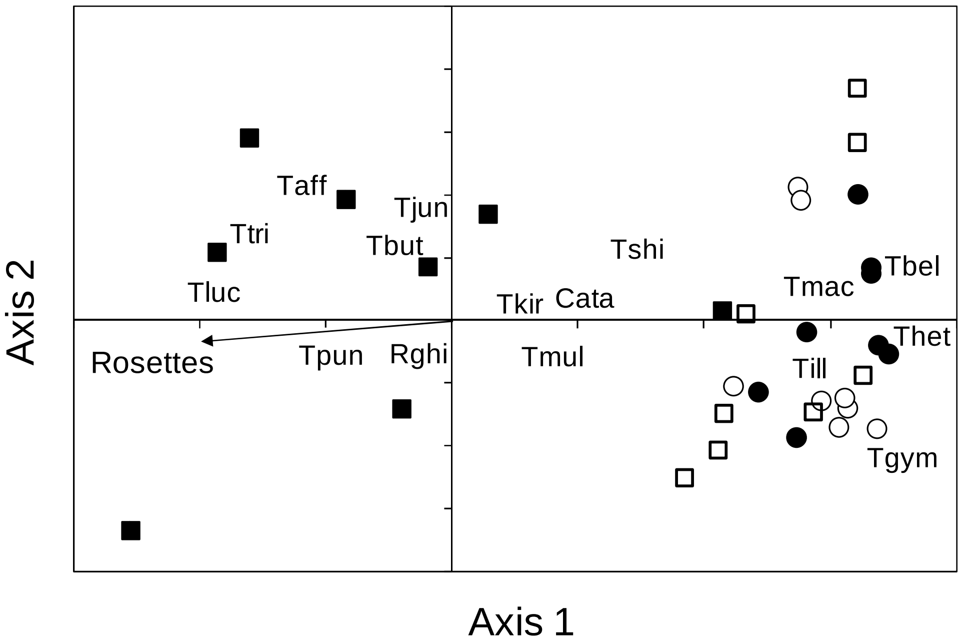

Fig. 4 Canonical Correspondence Analysis triplot for trees and bromeliads in four TMCF sites in central Veracruz, Mexico. Open circles are trees in Site 1; filled circles are trees in Site 2; open squares are trees in Site 3; filled squares are trees in Site 4. The vector is the significant explanatory variable; number of rosettes per tree. Acronyms for epiphytic bromeliads: Cata, *Catopsis* spp.; Tbell, *Tillandsia belloensis*; Tbut, *T. butzii*; Tdep, T. *deppeana*; Taff, *T.* aff. *fasciculata*; Tfol, *T. foliosa*; Rghi, *Racinaea ghiesbreghtii*; Tgym, *T. gymnobotrya*; Thet, *T. heterophylla*; Tjun, *T. juncea*; Tkir, *T. kirchhoffiana*; Tluc, *T. lucida*; Tmul, *T. multicaulis*; Tpun, *T. punctulata*; Tshi, *T. schiedeana*; Ttri, *T. tricolor*; Tmac, *T. macropetala*; Till, *Tillandsia* spp.

Implications for conservation

Our results indicate that even small TMCF fragments in Central Veracruz support high tree and epiphytic bromeliad richness and diversity. The high heterogeneity found among these forest fragments emphasizes the importance of maintaining as many fragments as possible, regardless of their size [19-21, 34]. First, extended primary forest areas are of vital importance since these represent the main source of propagules for the regeneration of numerous species of old growth TMCF, and second, many secondary forest components have the ability to colonize degraded areas, and their dispersal capacity is generally greater than that of the species typical of more advanced stages [16, 53, 54]. The extremely important role of even very small and degraded remnant TMCF fragments as reservoirs of biodiversity should therefore be fully considered in the design of forest management policies. Remnant TMCF such as these small fragments could play an important role in restoration initiatives. Conservation of TMCF in this region is chiefly supported by Payment for Environmental Services, reinforcement of community forestry, and educational campaigns to promote the cultural and natural values as well as the environmental services provided by TMCF [54].

Challenger and Dirzo [55] estimate that of the original cover of 3.1 million ha of TMCF in Mexico, only 28% remained by 2002. Of this remaining area, only 47.6% were primary forest, and thus degraded or secondary forests form the predominant vegetation. In the central region of Veracruz state, TMCF has suffered extensive transformation and currently exists only as remnant fragments, occupying less than 10% of the original area [56]. In the study area, the predominant landscape elements are young secondary forests, cleared grazing and cultivated areas, with small old-growth forest stands mainly on the highest and steepest slopes. In this area, coordinated efforts to maintain even small fragments and increase connectivity at the landscape level [39, 54] are of vital importance for TMCF biodiversity conservation.

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