



# Do Harvest Practices of Bromeliads and Forest Management in Sierra Norte of Oaxaca Have a Negative Effect on their Abundance and Phorophyte Preference?

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## ABSTRACT

The present study recorded inhabitants' traditional knowledge and uses of bromeliads and the phorophytes present in their ecosystems in two localities of Oaxaca. We also evaluated the effect of harvest practices on the abundance and distribution of the populations of these epiphytes on different phorophytes, considering the existence, or not, of a Forest Management Program. Structured interviews were conducted with 60 adults to identify the species of bromeliads of greater cultural importance (BGCI). We identified recurrent harvest sites (RHS) and occasional harvest sites (OHS) in order to estimate the abundance and phorophyte preference of BGCI. Traditional names and uses of epiphytes and phorophytes are described; it was identified that *Tillandsia deppeana*, *T. lucida* and *Catopsis occulta* had the highest BGCI in both localities. Their populations showed greater abundance values in OHS in both localities compared with RHS ( $\chi^2_{gl6} = 296.99$ ,  $p < 0.05$ ). *T. deppeana* and *T. lucida* were shown to prefer *Quercus elliptica*, while distribution of *C. occulta* showed a preference for *Q. rugosa* and *Pinus oocarpa*; however, phorophyte preference patterns of bromeliads may be influenced by the intensity of forest management. Decrease in abundance as the size category increased was recorded in three species, as well as the adult harvest. Finally, the inhabitants of both communities demonstrate similarities in their traditional knowledge, the intensity of harvest may be a factor influencing their abundance and preference of phorophytes, but also forest management programs determine the availability of bromeliads populations, due to the phorophytes specificity that some bromeliads exhibited.

**Keywords:** *Catopsis*; Ethnobotany; Host Preference; *Tillandsia*; Zapotec People.

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## SIGNIFICANCE STATEMENT

Bromeliads are one of the most important species used for ornamental and magic-religious purposes within local communities of Mexico. Because most of them are gathered from wild, concern on the effect of these practices on plant populations contributed to regulate them. For some decades, Mexican government has implemented forest management programs in order to provide economic income to local people through extraction forest resources and to protect them. However, the benefits of these programs on structure and composition of forests depends on how they are designed. This paper contributes to understand the cultural value of these species inside two indigenous communities of Mexico and to understand the effect of harvest practices on some ecological parameters of bromeliads populations, as well as the effect of forest management programs on bromeliads availability, based on the concept of phorophyte preference, which seems opposite to the forest species proposed in these programs.

## INTRODUCTION

Through their history, human populations have interacted with other living organisms and as with environmental components, which has led to the construction of traditional knowledge of the natural world. This traditional knowledge is defined as the perceptions, beliefs, customs, forms of uses and management of natural resources and the role that play inside each culture (Ticktin et al. 2007; Lepofsky 2009; Luna-José and Rendón-Aguilar 2012). One of the botanical families that reflect this traditional knowledge, because it has been valued for its attributes (e.g., forms, colours, size) is the Bromeliaceae family. A recent synthesis on the use of bromeliads in Latin America indicates that 78 species are used to meet different social needs such as medicine, food, ceremonial uses, ornamental uses, natural fibers or living fences (Hornung-Leoni 2011).

In Mexico, people have included the Bromeliaceae family within their cultural practices since pre-Hispanic times, as has been reported for species of the genera *Aechmea* Ruiz & Pav., *Bromelia* L., *Catopsis* Griseb., *Pitcairnia* L'Hér., *Tillandsia* L., and *Vriesea* Lindl. (Bennett 2000; Hornung-Leoni 2011). Currently, different species of bromeliads are used in various regions of the country, for different purposes. In Tamaulipas, people use *B. balansae* to make traditional drinks and sweets, while in the region of Huasteca, *A. bracteata* (Sw.) Griseb. and *T. imperialis* E. Morren ex Mez are used for medicinal purposes, and in Hidalgo, leaves juice of *Hechtia podantha* Mez is used to curd cheese (Villavicencio and Pérez 2006). In Oaxaca, in the southeast Mexico, the largest number of bromeliad species in the country has been recorded (Espejo-Serna et al. 2004; Espejo-Serna and López-Ferrari 2018). Like in other regions, bromeliads in Oaxaca have been linked to the traditions of diverse ethnic groups, mainly in festivities or religious events as ornamental features, as they are considered plants of great cultural beauty (Sandoval-Bucio et al. 2004; Mondragón and Villa-Guzmán 2008; Mondragón 2008; Rendón-Aguilar 2017). In addition to

this important cultural relationship, bromeliads have a fundamental ecological role in terrestrial ecosystems, as they are essential organisms maintaining the relative humidity of forests as well as providing food and habitat to a wide variety of living beings (Mondragón-Chaparro and Cruz-Ruiz 2008; Mondragón and Cruz 2009; Hornung-Leoni 2011).

Despite the cultural and ecological importance of bromeliads, these plants face negative anthropic factors that severely affect survival of their populations. The high demand for bromeliads in magical-religious festivities and for ornamental purposes at the local or regional level has provoked an intense gathering of wild individuals with flowers, which prevents them from completing their life cycle, including reproduction (Guess and Guess 2002; Beutelspacher and Farrera 2007; Haeckel 2008; Hernández-Cárdenas et al. 2014; Jiménez-López et al. 2019). Some species that face these risks are *Tillandsia macdougallii* L.B. Sm., *T. violacea* Baker, *T. juncea* (Ruiz & Pav.) Poir., *T. multicaulis* Steud., and *T. punctulata* Schltld. & Cham. in Veracruz (Winkler et al. 2007; Mondragón-Chaparro and Ticktin 2011) and *Catopsis berteroniana* (Schult. & Schult. f.) Mez, *T. gymnobotrya* Baker, *T. carlos-hankii* Matuda, and *Viridantha plumosa* (Baker) Espejo in Oaxaca (Mondragón and Villa-Guzmán 2008).

Changes in plant cover for agricultural and forestry use have also decreased the abundance and distribution of many species of this botanical family, because 225 of the 422 bromeliad species registered in Mexico are epiphytic; that is, they need to stay on trees (phorophytes) to survive (Espejo-Serna et al. 2004; Espejo-Serna and Lopez-Ferrari 2018). Wolf (2005) reports that in a pine-oak forest in southern Mexico (Chiapas), deforestation is directly related to the decrease in epiphytic biomass, including bromeliads. Further, it has been reported that certain species of phorophytes exhibit morphophysiological characteristics that favor the establishment and growth of epiphytes, as Ramírez-Martínez et al. (2018) demonstrated with *Tillandsia carlos-hankii*, an epiphyte that is preferably established on individuals

of *Quercus rugosa* Née, *Q. laurina* Bonpl., and *Rapanea juergensenii* Mez in a pine-oak forest in the state of Oaxaca.

In Oaxaca, as in other parts of Mexico, populations of different bromeliad species are subject to human pressures, like intensive deforestation. This state has the third-highest deforestation rate in Mexico, with cuttings exceeding 24 thousand ha for year (Velázquez et al. 2003), which causes a significant loss of trees that epiphytic bromeliads and other organisms need to survive. Of equal importance are the gathering practices of reproductive individuals, which are used in traditional festivities (Mondragón 2008; Solano et al. 2010; Rangel-Landa et al. 2016).

In this context, the present study seeks to understand the following questions: What is the traditional knowledge that the inhabitants of two localities of the Sierra Norte de Oaxaca have on the species of bromeliads and the phorophytes that exist in their ecosystems? Does the intensity of harvest influence the distribution of bromeliads on the phorophytes? Do harvest practices affect abundance and distribution of the populations of these epiphytes? Do forest management practices affect bromeliad and phorophytes populations? This research showed the negative effect of harvest practices on abundance and phorophyte preference of bromeliads, as well as the potential importance to incorporate traditional knowledge and scientific results in the development of regulations for forest management and conservation programs.

## MATERIAL AND METHODS

### Study area

The study was carried out in two localities of the mountainous system of the Sierra Norte de Oaxaca: San Juan Tabaa (SJT), which is located at coordinates 17°17' – 17°21' N and 96°11' – 96°15' W, between 500 and 2,100 m a.s.l. elevation, and occupies an area of 2,769 ha (Figure 1). Santo Domingo Yojovi (SDY), which belongs to the municipality of San Andrés Solaga, is located at coordinates 17°17' – 17°18' N and 96°12' – 96°13' W, between 500 and 2,400 m a.s.l., covering an area of 1,205 ha (Castellanos et al. 2005). Both areas are characterized by pine-oak, oak, and mountain cloud forests (INEGI 2011) (Figure 1).

The inhabitants of this region are indigenous people belonging to the Zapotec culture, speaking both Zapotec and Spanish, and have inhabited the area since before the arrival of Spanish people in 1521 (Castellanos et al. 2005; Bautista 2017). Therefore, we would expect within these communities an extensive and deep knowledge of their local environment and, in particular, bromeliads, despite the current

changes in the use of their natural resources due to forest management programs implemented in recent decades (CONAFOR 2014) that have impacted their perception and management of forests.

SJT has had a timber Forest Management Program authorized by the National Forestry Commission since 2010 (CONAFOR 2014). With this program, people in the community are prohibited from harvesting wild plants, such as bromeliads, and are only allowed to collect firewood—which is still the main source of fuel in homes—at authorized sites. However, as detailed below, we identified recurrent harvest in the proximity of urban area in both. In contrast, SDY, at the time of this study, lacked of a Forest Management Program, so the municipal authority allows people to harvest bromeliads, firewood and other resources; wood harvesting is carried out in authorized areas within the community.

### Data collection and analysis

In July 2015, an exploratory field trip was conducted to present the project to the local authorities, in order to corroborate previous information about the existence of harvest practices of bromeliads in these communities (Rendón-Aguilar 2017) and to obtain formal permission to carry out the research. From this exploration we were informed of the dynamics of the use of bromeliads, the existence of different bromeliads with variation in their phenology and the differences of forest management strategies between the two communities. Later field trips were then undertaken quarterly, from September 2015 to April 2017. Voucher specimens of different useful bromeliads were obtained in triplicate. In the case of epiphytes, their phorophytes was collected, also in triplicate. Specimens were processed according to the methods proposed by Aguirre (1986) and Wendt (1986), and deposited in the herbaria UAMIZ (Thiers [continuously updated]). They were taxonomically determined by experts of each family.

### Traditional ecological knowledge, uses and management

To record inhabitants' traditional ecological knowledge about the management and use of bromeliads and phorophytes, 30 interviews were conducted in each locality (Add File 1). The following questions were asked:

- What are the names and features of bromeliads and phorophytes that people recognize?
- What is the cultural importance of bromeliads for the inhabitants?

- What are the uses and management of this species?
- Where do they get bromeliads?
- Do bromeliads have ecological functions for the inhabitants?
- How did they learn about bromeliads?

Adding to these interviews, we searched for people recognized in their communities as bromeliad connoisseurs (collaborators), through the snowball method proposed by Goodman (1961) and Bernard (2006). The identification of bromeliad connoisseurs was very important, as these individuals helped us to obtain information about the local names of bromeliads and trees, their uses and the importance of these natural resources in the local culture. In total, 60 semi-structured interviews were accomplished for this investigation. Bromeliad harvest practices were documented through participative observation with local women.

### Bromeliads of greater cultural importance (BGCI)

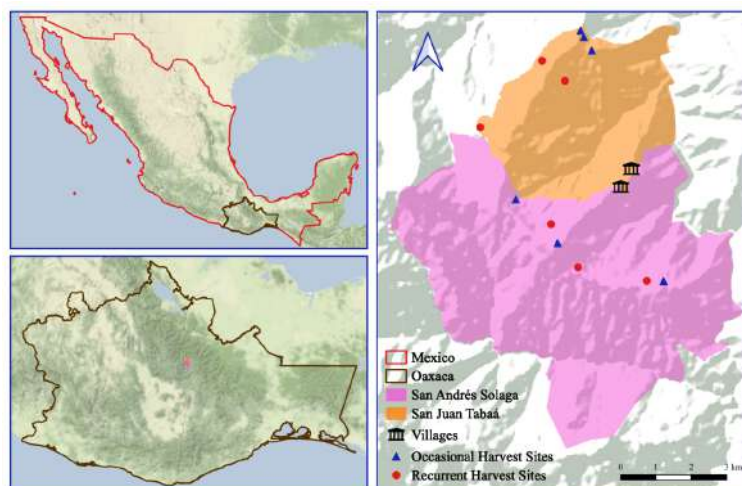
The outstanding value method was used to identify BGCI and thus evaluate only bromeliad populations of those species highlighted through interviews. This method considered the order and frequency in which species were mentioned or described by the informants in a free list. Those species more mentioned, as well as those mentioned in the first places, were considered BGCI (Trotter and Logan 1986; Quinlan et al. 2002).

### Choice of sampling sites

Based on interviews, we identified those places, forbidden or not, where the people gathered firewood and they took advantage to harvesting bromeliads, even in SJT, where the bromeliad harvest was restricted, so we asked about where firewood were usually harvested, as well as places where it is difficult to get them. From this information, two different sites were chosen in each location: i) recurrent harvest sites (RHS), classified as being easily accessible areas due to their proximity to rural roads (terracerías and veredas) to carry out the harvest of firewood, and ii) occasional harvest sites (OHS), areas that due to their difficulty of access are very infrequently visited, as extraction of firewood was not allowed (Figure 1). Three sampling plots were established for RHS and three plots for OHS in each of the two locations, for the evaluation of a total of 12 plots. Each plot was 60 m × 10 m and was divided into six subplots of 10 m × 10 m. Of these, only the first, third and fifth subplots were sampled. We recorded the following information:

### Tree community

Trees with a diameter basal area (DBH) > 7 cm or more were marked and measured with a diametric tape. To describe community structure, we calculated the following variables: i) frequency (F), the number of individuals per species in the sampled area; ii) basal area (AB), obtained as  $\pi(\text{DBH}/2)^2$ , iii) volume of the canopy (VC): in the case of *Pinus* spp. trees, volume was calculated as a cone; volume of the rest of the tree species was calculated as a cylinder, then relative



**Figure 1.** Study Area. Top left, Mexico; Bottom left, State of Oaxaca. Right, municipalities of San Juan Tabaá (SJT) (orange) and San Andrés Solaga (pink), in the Sierra Norte of Oaxaca. Urban areas (villages) of both localities, occasional harvest sites (OHS) and recurrent harvest sites (RHS) are indicated (Elaborated by: LA Bernal-Ramírez).



values were obtained (Bernal et al. 2005; Ramírez-Martínez et al. 2018).

## Abundance of bromeliads

In each tree, the number of individuals of the BGCIs were counted, dividing them into approximate size categories, defined as follows: i) seedling: < 5 cm; ii) juvenile 1: > 5 cm and < 15 cm; iii) juvenile 2: > 15 cm and < 25 cm; iv) adult: > 25 cm or with presence of inflorescence regardless of size; and v) with the presence of fruits and seeds. An  $\chi^2$  test between absolute abundance and RHS and OHS respectively, in both SJT and SDY, was conducted in order to test the null hypothesis that absolute abundance is independent of forest management.

## Preferential occupation of phorophytes

The total number of trees occupied by each species of BGCIs was compared through a  $\chi^2$  test in order to assess whether the distribution of bromeliads on different species of phorophytes was simply due to the availability of tree individuals, independent of the species they belong to (which would correspond to the distribution expected by chance), or if said distribution differed from what would be expected by chance, in which case it could be concluded that there would be preferences for some species of phorophytes over others, or that some phorophytes would be limiting (Bernal et al. 2005; Ramírez-Martínez et al. 2018). Subsequently, a Haberman residue analysis (1973) was carried out to identify which species of phorophytes were preferred or avoided, by the bromeliads studied. Furthermore, to avoid a statistical error type I, a Bonferroni correction was performed, adjusting the threshold value of p to 0.0125 (Ramírez-Martínez et al. 2018). To evaluate these results, data from the three repetitions of each site (RHS and OHS) were joined.

## RESULTS AND DISCUSSION

### Traditional ecological knowledge, uses and management

In SJT, 12 species of bromeliads were recorded, of which eight were used and named in Zapotec by the inhabitants. We categorized uses of bromeliads and phorophytes according to people's answers. Uses correspond to ceremonial, ornamental and commercial (Tables 1 and 2). Ten species of phorophytes belonging to five different botanical families were identified. The inhabitants recognized eight tree species with Zapotec nomenclature; seven species had at least one local use, and only *Clethra occidentalis* (L.) Kuntze had

no use (Table 1).

SDY showed higher richness of bromeliads and their respective phorophytes, with 14 and 11 species, respectively. *Racinaea adscendens* (L.B. Sm.) M.A. Spencer & L.B. Sm. and *R. ghiesbreghtii* (Baker) M.A. Spencer & L.B. Sm. did not have any use, but they were clearly recognized by inhabitants, who named both species with the same Zapotec name (shabna ghaá) (Table 1).

In SDY, 14 inhabitants were recognized as connoisseurs of bromeliads, while in SJT, collaborators identified nine. Traditional ecological knowledge that people have has been acquired through their parents and grandparents, although in both communities some collaborators mentioned that the same local experts have enriched their knowledge about the names or habitats of bromeliads. In both communities, visual or tactile recognition is used to distinguish bromeliads and phorophytes (Tables 1 and 2), as in the case of *Tillandsia lucida* E. Morren ex Baker, whose name in Zapotec refers to the texture of the inflorescence, or *Catopsis occulta* Mart.-Correa, Espejo & López-Ferr., whose name describes the color of its inflorescence (Table 1).

With respect to phorophytes, it was observed that despite the spatial proximity between one locality and another, the pronunciation and sometimes the interpretation of a single species may differ. Such is the case of *Quercus elliptica* Née, whose name in SJT is interpreted as a white oak (chiche), while in SDY it is perceived as a tree whose bark is similar to the color of ash (shoyeché) (Table 2). Collaborators also recognize that bromeliads play an important role in ecosystem functions, such as collection and maintenance of water supply in forests, "housing" other organisms and providing beauty to their forests.

In both localities, bromeliads are used for ceremonial, ornamental and commercial purposes (Table 1); while the trees can be used preferably for fuel, as in the case of *Quercus obtusata* Bonpl. and *Pinus chiapensis* (Martínez) Andresen, others are used for construction and as tools for agriculture, such as *Q. rugosa* Née, *Q. scytophylla* Liebm., and *P. oocarpa* Schiede ex Schltdl., and still others give shade to coffee plantations, such as *Agarista mexicana* (Hemsl.) Judd (Table 2). In particular, in SJT, where harvest of bromeliads is restricted, it was observed that in two consecutive years, during the Holy Week celebration (religious holiday of Mexico), the inhabitants harvested bromeliads in order to decorate five floral arcs with *Tillandsia lucida*, *T. deppeana* Steud. and *T. prodigiosa* (Lem.) Baker (Figure 2a). Unfortunately, it was not possible to go with them to document this process. On the other hand, in SDY, it was possible to participate with women in the harvest of bromeliads (Figure 2b) in different moments.

**Table 1.** Names and Uses of Bromeliads recorded in San Juan Tabaá (SJT) and Santo Domingo Yojovi (SDY).

REF. NO	BROMELIAD SPECIES	ZAPOTEC NAME (MEANING IN SPANISH)		USES
		SJT Shabna	SDY Na	
	<b>Bromeliad Family Bromeliaceae</b>			
11, 16	<i>Catopsis occulta</i> Mart.-Correa, Espejo and López-Ferr.		gaché(yellow)	Ceremonial, Ornamental, Commercial
29, 83	<i>Catopsis nutans</i> (Sw.) Griseb.		unnamed	
36, 4	<i>Catopsis paniculata</i> E. Morren		unnamed	
45, 64	<i>Catopsis subulata</i> L.B. Sm.		xhua (similar to corn kernels)	Ceremonial, Ornamental, Commercial
75	<i>Racinaea adscendens</i> (L.B. Sm.) M.A. Spencer and L.B. Sm.	Not found	Ghaá(green)	
28	<i>Racinaea ghiesbreghtii</i> (Baker) M.A. Spencer and L.B. Sm.			
17, 44	<i>Tillandsia deppeana</i> Steud.	xhiga  (flowers growing from the same place)	rahaza	Ceremonial, Ornamental, Commercial
46, 50	<i>Tillandsia gymnotrya</i> Baker		zacuan (similar to bean flower, recognized as quarantine)	Ceremonial, Ornamental, Commercial
60, 77	<i>Tillandsia kirchhoffiana</i> Wittm.		unnamed	
62, 65	<i>Tillandsia lucida</i> E. Morren ex Baker		zaá (grease like texture)	Ceremonial, Ornamental, Commercial
9, 32	<i>Tillandsia multicaulis</i> Steud.	rhabio (small flowers distributed in a circular structure)	yeta (flowers distributed in a similar form like tortilla)	Ceremonial, Ornamental, Commercial
51, 61	<i>Tillandsia prodigiosa</i> (Lem.) Baker	soshchjarha/deé (flower growing down /leaves color similar to hash)	yesha (from similar to cob)	Ceremonial, Ornamental, Commercial
12, 23	<i>Tillandsia punctulata</i> Schltld. and Cham.	shichaxhio (duster like leaves)	yeche (spines like leaves)	Ceremonial, Ornamental, Commercial
3, 37	<i>Werauhia werckleana</i> Mez		unnamed	

**Legend:** Zapotec names are indicated first and in parenthesis are the meaning in Spanish.

**Table 2.** Names and uses of tree species (phorophytes) recorded in San Juan Tabaá (SJT) and Santo Domingo Yojovi (SDY).

REF. NO	Tree species (phorophytes)	ZAPOTEC NAME (MEANING IN SPANISH)		USES
		SJT	SDY	
	<b>Tree species (phorophytes)</b>	<b>Shaga</b>	<b>Yaga</b>	
	<b>Family Clethraceae</b>			
14, 71	<i>Clethra occidentalis</i> (L.) Kuntze		becoxhozé (shell like trunk)	
	<b>Family Ericaceae</b>			
49, 70	<i>Agarista mexicana</i> (Hemsl.) Judd.	feela (eagle stick)	begha (eagle stick)	Coffee shadow, fuel, construction
5, 52	<i>Gaultheria erecta</i> Vent.		unnamed	
1, 20	<i>Vaccinium aff. leucanthum</i> Schltdl.		unnamed	
	<b>Family Fagaceae</b>		benio(oak)	
31, 43	<i>Quercus elliptica</i> Née	chiche (white)	shoyeché (ash colored bark)	Fuel, plowing tool
8, 33	<i>Quercus obtusata</i> Bonpl.	xnha (red bark)	unnamed	Fuel, construction, natural dye, plowing tool
53, 72	<i>Quercus rugosa</i> Née	xhogaveo (turdy wood)	sogaveo (strong woof)	Fuel, construction
7, 47	<i>Quercus scytophylla</i> Liebm.	shaxho (earth colored bark)	yayo (earth colored bark)	Fuel, construction
	<b>Family Phyllonomaceae</b>			
39, 63	<i>Phyllonoma laticuspis</i> (Turcz.) Engl.	shechhe (yellow)	yeche (yellow)	Fuel
	<b>Family Pinaceae</b>			
4, 54	<i>Pinus chiapensis</i> (Martínez) Andresen	zaa (grease like texture)		Fuel, construction
22	<i>Pinus oocarpa</i> Schiede ex Schltdl.	Not found	zigxhag (short)	Fuel, construction

**Legend:** Zapotec names are indicated first and in parenthesis are the meaning in Spanish.

## Identification of Bromeliads of greater cultural importance (BGCI)

According to the outstanding value method, *Catopsis occulta*, *Tillandsia deppeana* and *T. lucida* had the highest BGCI for the inhabitants of both locations, and they were always mentioned first (Table 3).

## Choice of sampling sites

According to SJT collaborators, the OHS were 3.5 km from downtown, while RHS were 3.8 km, on average. In the case of SDY, OHS were 2.87 km away from the downtown, while the RHS were 2.64 km away from the trails. Even though the RHS were apparently further away in both localities, there is more accessibility due to the presence of roads (terraceras and veredas). Temperate forests (pine, oak and oak-pine, Add File 2) were the main types of vegetation in the sampling sites.

## Tree community

**OHS:** In SJT, OHS showed a tree density of 62 individuals/ha, belonging to five families, six genera and nine species; the most abundant were *Quercus elliptica* and *Q. obtusata*. *Q. elliptica* and *Q. rugosa* exhibited the greatest relative basal area, while *Q. elliptica* and *Q. scytophylla* accounted for the highest relative volume of the canopy (Add File 3). SDY, in contrast, had 80 tree individuals/ha in OHS, belonging to four families, four genera, and six species. *Q. elliptica* was the most abundant species, with the greatest basal area and the highest relative volume of the canopy (Add File 3).

**RHS:** In SJT, RHS had a lower tree density, with 44 individuals/ha, belonging to three families, four genera, and five species, with *Pinus chiapensis* and *Quercus obtusata* being the most abundant. Furthermore, these species presented the largest basal areas and canopy volumes (Add File 3). In SDY, RHS had the lowest tree density, with only 20 individuals/ha, belonging to two botanical families, two genera, and three species: *Clethra occidentalis*, *P. chiapensis* and *P. oocarpa*, *Pinus* exhibited the highest values of basal area and volume of canopy (Add File 3).

## Abundance of bromeliads

**OHS:** In both localities, *Tillandsia deppeana*, *T. lucida* and *Catopsis occulta* registered great abundance in the smallest size categories (Seedling, Juvenile 1 and Juvenile 2). However, in the larger size categories (Adult, Fruit/Seed), abundance of these species decreased (Figure 3a, 3b).

**RHS:** In SJT, abundance of the mentioned bromeliads decrease compared to that recorded for

OHS (Figure 3c, 3d). However, individuals of different size categories, from seedlings to individuals with presence of fruits and seeds, were recorded. In SDY, RHS had the lowest abundance of all the sites. Additionally, only adult individuals were recorded for *Tillandsia deppeana* (Figure 3d). The  $\chi^2$  test showed significant differences ( $\chi^2$  gl6 = 296.99,  $p < 0.05$ ) between OHS and RHS in SJT and SDY.

## Preferential occupation of phorophytes

**OHS:** Bromeliads exhibited a significant preference for some phorophytes in OHS of SJT ( $\chi^2$  *Tillandsia deppeana* = 197.33;  $\chi^2$  *T. lucida* = 167.1;  $\chi^2$  *Catopsis occulta* = 483.2; gl = 5,  $p < 0.0001$ ) and SDY ( $\chi^2$  *T. deppeana* = 113.75;  $\chi^2$  *T. lucida* 60.13;  $\chi^2$  *C. occulta* = 235.11; gl = 4,  $p < 0.0001$ ), regardless of their frequency. For example, in SJT, the tree species with high frequency were *Quercus rugosa* and *Q. obtusata*. However, they were limiting phorophytes for *T. deppeana*, which exhibited preference for *Q. elliptica* and *Q. scytophylla*. *T. lucida* showed preference for *Q. elliptica* and *Q. obtusata*, *Q. rugosa* and *Phyllonoma laticuspis* were limiting. *C. occulta* preferred *Q. rugosa* for its establishment, while *Q. elliptica* and *Q. obtusata* were limiting phorophytes for this bromeliad (Table 4).

In SDY, BGCI were found in 80 individual tree hosts as well as in the floor, but again, they exhibited phorophyte preferences. *Tillandsia deppeana* preferred *Quercus elliptica*, while *Q. scytophylla* and *Pinus oocarpa* were limiting phorophytes. *T. lucida* occupied five of the six phorophyte species recorded in OHS, but showed preference only for *Q. scytophylla* and *P. oocarpa* was a limiting phorophyte. *C. occulta* preferred *P. chiapensis* and *P. oocarpa*, even when these species represent only 10% of the total trees at OHS (Table 4).

**RHS:** In SJT, BGCI exhibited a significant preference for some phorophytes ( $\chi^2$  *T. deppeana* = 31.19;  $\chi^2$  *T. lucida* = 27;  $\chi^2$  *C. occulta* = 46.72; gl = 4,  $p < 0.0001$ ). The statistical analysis showed that *T. deppeana* prefer *Q. obtusata* and *Q. rugosa*. *T. lucida* had preference for *Q. elliptica* and *Q. rugosa*, while *C. occulta* prefer *Q. obtusata* and *Q. rugosa*.

In SDY, *T. deppeana* exhibited a significant preference for *P. chiapensis* ( $\chi^2$  *T. deppeana* = 18.56; gl = 1,  $p < 0.0001$ ), while *P. oocarpa* was a limiting phorophyte (Table 4). *C. occulta*, and *T. lucida* showed a random distribution in the trees that were available at that site ( $\chi^2$  *T. lucida* = 1.05;  $\chi^2$  *C. occulta* = 3.24; gl = 1,  $p < 0.0001$ ), it means, that the distribution of bromeliads on phorophytes was simply due to the availability of tree individuals.





**Figure 2.** A) Ornamental arc elaborated with flowers of *T. lucida*, *T. deppeana* y *T. prodigiosa* in SJT. B) Participative observation with women of SDY gathering bromeliads.

**Table 3.** Values of frequency (f) and order of mention (o) of bromeliads by the inhabitants of SJT and SDY

Species	SJT		SDY	
	f	o	f	o
<b><i>Tillandsia lucida</i></b>	26	0.68	25	0.61
<b><i>Catopsis occulta</i></b>	24	0.54	27	0.68
<b><i>T. deppeana</i></b>	15	0.36	20	0.43
<i>T. multicaulis</i>	7	0.11	4	0.11
<i>T. punctulata</i>	3	0.05	10	0.13
<i>T. gymnotrya</i>	3	0.05	6	0.10
<i>T. prodigiosa</i>	1	0.01	8	0.11
<i>C. subulata</i>	0	-	3	0.05
<i>T. butzii</i>	0	-	2	0.03
<i>Racinaea</i> sp.	0	-	2	0.03

**Legend:** The bromeliads with the highest values are indicated in bold.

## DISCUSSION

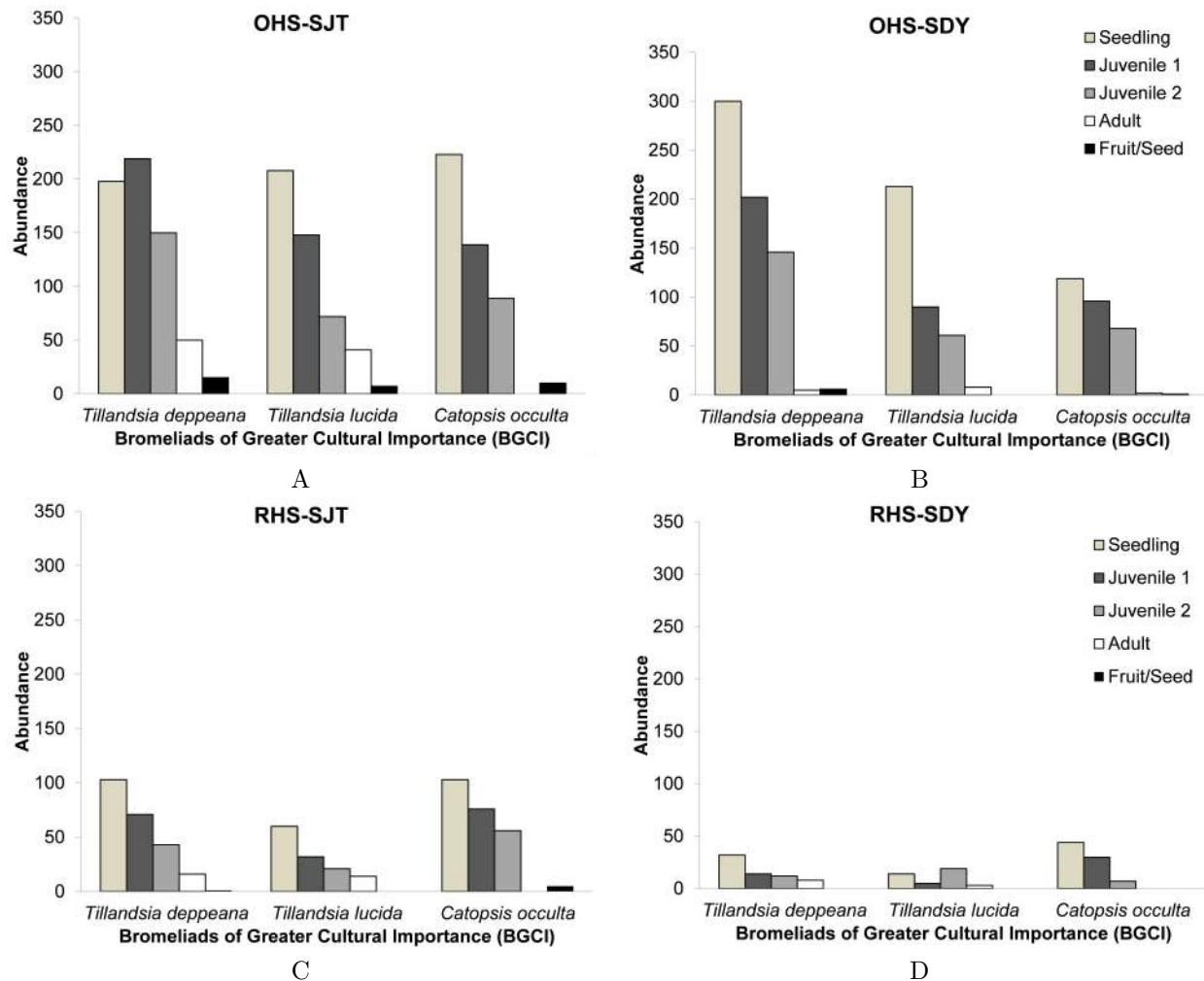
The cultural and economic importance of bromeliads in different communities of Oaxaca is notorious, as they are employed to magical-religious ceremonies, as an ornament in orchards, and even have non-material uses, like the perception of the “beauty of forest” (Mondragón et al. 2016; Riveros-Cañas et al. 2016; Rendón-Aguilar 2017). This is reflected in several works that have recorded this traditional ecological knowledge acquired over time by different societies as a result of continuous interaction with bromeliads (Mondragón and Villa-Guzmán 2008; Luna-José and Rendón-Aguilar 2012).

According to Castellanos et al. (2005) and Bautista (2017), SJT and SDY are Zapotec communities that share a traditional environmental knowledge; in this research we saw it in the same uses and a similar management of bromeliads and trees, although there are some nomenclatural variants in the tradi-

tional classification of bromeliads. Basic morphological attributes are the main components of traditional ecological knowledge of these species, as has been reported for other ethnoclassifications (Newmaster et al. 2006). However, in the present study, inflorescence texture was registered as another trait used to distinguish *Tillandsia deppeana*.

Collaborators of both communities mentioned that bromeliads are beneficial for forests, since they help to collect and store rainwater, as well as housing and providing food to different animals. This view contrasts with that reported in some communities in Veracruz, where bromeliads are perceived as parasites in the ecosystems they inhabit (Toledo-Aceves et al. 2014a,b).

During the present research, we noted that in both communities, people show preference for some bromeliads. Species of *Tillandsia* recorded the greatest number of useful species, as occurs in other localities of Oaxaca, and also in other states of Mex-



**Figure 3.** Abundance of seedling, juvenile 1, juvenile 2, adult and fruit/seed categories of *Tillandsia deppeana*, *T. lucida* and *Catopsis occulta* in A) Occasional Harvest Sites in San Juan Tabaá (OHS-SJT); B) Occasional Harvest Sites in Santo Domingo Yojovi (OHS-SDY); C) Recurrent Harvest Sites in San Juan Tabaá (RHS-SJT) and D) Recurrent Harvest Sites in Santo Domingo Yojovi (RHS-SDY).

ico (Bennett 2000; Wolf and Konings 2001; Sandoval-Bucio et al. 2004; Beutelspacher and Farrera 2007; Flores-Palacios and Valencia-Díaz 2007; Mondragón 2008; Mondragón and Villa-Guzmán 2008; Hornung-Leoni 2011; Jiménez-López et al. 2019). It should be noted that local merchants of each community are important actors in the transmission of knowledge about bromeliads, since 30% of the collaborators said that merchants teach them about traditions, names, phenology as well as ecological aspects of the plants (e.g., preference of phorophytes).

### Bromeliads of greater cultural importance (BGCI)

*Catopsis occulta*, *Tillandsia deppeana*, and *T. lucida* were identified as the bromeliads with the greatest cultural importance and the highest beauty values

in both localities, and they were also sold with the highest prices in the local market. These factors could be related with the overlap of their flowering period with some local religious holidays, in addition to the perception of beauty that collaborators of both localities share about these species, as has been suggested in other studies (Flores-Palacios and Valencia-Díaz 2007; Haekkel 2008; Mondragón and Villa-Guzmán 2008).

### Abundance of bromeliads

RHS in both localities recorded low abundance of BGCI compared to OHS, which evidenced the recurrent harvest activities of these species in those places, due to their accessibility and because they take advantage when harvest firewood; also, in these areas forest use is allowed, which in consequence causes modifica-

**Table 4.** Preferential occupation of phorophytes of *Tillandsia deppeana* (Td), *T. lucida* (Tl) y *Catopsis occulta* (Co) in Occasional Harvest Sites (OHS) and Recurrent Harvest Sites (RHS) in San Juan Tabaá (SJT) and Santo Domingo Yojovi (SDY).

PHOROPHYTE	SJT		SDY	
	OHS	RHS	OHS	RHS
<i>Quercus elliptica</i>	* Td, Tl, Co	* Tl	* Td, Co	
<i>Quercus obtusata</i>	* Td, Tl, Co	* Td, Co		
<i>Quercus rugosa</i>	* Td, Tl, Co	Td, Tl, Co		
<i>Quercus scytophylla</i>	* Td, Co		* Td, Tl, Co	
<i>Phyllonoma laticuspis</i>	* Td, Tl, Co			
<i>Pinus chiapensis</i>	* Co	* Td	* Co	* Td
<i>Pinus oocarpa</i>			* Td, Tl, Co	* Td

**Legend:** Initial letters of bromeliads that exhibited preference for any phorophyte are indicated in normal, and in italic when phorophyte represented a limiting resource for bromeliads. Those phorophytes that had a relative frequency > 5% in each sampled site are indicated with \*.

tions in environmental conditions and alters the availability of phorophytes (Barthlott et al. 2001; Wolf and Konings 2001; Wolf 2005; Toledo-Aceves et al. 2014a).

In general terms, there was greater abundance of adult and reproductive bromeliads in SJT than in SDY; in addition, it was observed that in OHS, and RHS of SDY, the number of seedling, juveniles and adult specimens was lower, which suggests that harvest practices have an important negative effect on bromeliad populations. It is likely that the absence of a Forest Management Program has negatively influenced the bromeliad populations. In the case of SJT, the Forest Management Program has influenced the maintenance of bromeliad and phorophyte populations.

### Preferential occupation of phorophytes

It has been documented that some bromeliad species have preferences for certain phorophytes (Wolf and Konings 2001; Bernal et al. 2005; Ramírez-Martínez et al. 2018). Wagner et al. (2015) suggested that a strong specificity of host opens up the possibility of sympatric speciation and may allow species to coexist in a complementary niche. This assumption is supported by the fact that both species of *Tillandsia* present in OHS in SJT, prefer *Quercus elliptica*, and are limited to colonize *Q. obtusata*, *Q. rugosa* and *Phyllonoma laticuspis*, so they could be

considered sympatric species; in contrast to *Catopsis occulta*, which preferred *Q. rugosa* and *P. laticuspis* and were limited in *Q. elliptica* and *Q. obtusata*.

Even when the specificity of the phorophyte is still unclear (Moffett 2000; Callaway et al. 2002; Bernal et al. 2005; Martínez-Meléndez et al. 2008; Wagner et al. 2015; Zotz 2016), it was evident that in both sampling sites, OHS and RHS, and in both localities, oaks were recorded as the tree species with the highest presence of BGCI, which is consistent with other papers (Castro et al. 1999; Callaway et al. 2002; Wolf 2005; Toledo-Aceves et al. 2014a), where *Quercus* spp. are mentioned as good host trees due to the ability of their bark to retain water and the ease of epiphytic seeds to anchor in them.

In the context of the Forest Management Plan by CONAFOR (2014) in SJT, our results are relevant because the main forest species considered in this program is *Pinus chiapensis*, and part of the proposed management includes total elimination of other species. Although this program could be successful in obtaining an adequate volume of wood from *P. chiapensis*, it could modify the composition and structure of these ecosystems, as well as transform the habitat for bromeliads and, in consequence, decrease their species richness (Barthlott et al. 2001; Merwin et al. 2003; Wolf 2005).

## CONCLUSION

The present study showed the negative effect of harvest practices on abundance and phorophyte preference of those bromeliads with the highest BGCI: *Tillandsia deppeana*, *T. lucida* and *Catopsis occulta*, in both locations where the study was developed, SJT and SDY. OHS presented a greater abundance of BGCI bromeliad species compared to RHS in both localities, regardless of the existence of a Forest Management Program (i.e., SJT). In general terms, *T. deppeana* and *T. lucida* prefer *Quercus elliptica* as phorophytes, while *C. occulta* showed preference for *Q. rugosa* and *Pinus oocarpa*. However, in places with intensive harvest practices, restrictive availability of phorophytes could be the main factor that determines bromeliads' phorophyte preferences. The existence of a Forest Management Program in SJT could explain the difference in the abundance of adult and reproductive bromeliads, but it has a negative effect on the availability of phorophytes because this program includes elimination of any species other than *Pinus chiapensis*. We propose a revision of this program in order to diversify forest management, ensure species richness, including epiphytes, like bromeliads. To avoid the loss of traditional knowledge of bromeliads, we propose to assign some areas inside these locations where inhabitants can obtain them, but also to promote their presence in the forest through propagation practices.

## FUNDING

This work was supported by Consejo Nacional de Ciencia y Tecnología (CONACYT), Universidad Autónoma Metropolitana Iztapalapa (UAMIZ) throughout the Master's Program in Biology and a scholarship number 425428 to the main author.

## ACKNOWLEDGEMENT

The authors express their total gratitude to the following people: The inhabitants of San Juan Tabaá and Santo Domingo Yojovi, especially to the Local Governments and the Zapotec translator Mr. Eleuterio Lorenzo Ruiz. Dr. Susana Valencia-Ávalos, Dr. Nancy Martínez-Correa and Jesús Ricardo de Santiago Gómez for the taxonomic determination of plants. Dr. David Bravo-Avilés for the field support and comments on this research. Luiz Alberto Bemal-Ramírez for elaborated the map of Study Area in this manuscript. UAMIZ Herbarium curator and researchers for technical support.

## DATA AVAILABILITY

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## CONTRIBUTION STATEMENT

Conceived of the presented idea: YVC, BRA, AES.  
Carried out the experiment: YVC, BRA.  
Carried out the data analysis: YVC, BRA, AES.  
Wrote the first draft of the manuscript: YVC, BRA.  
Review and final write of the manuscript: BRA, AES.  
Supervision: BRA, AES.

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**Received:** 06 August 2020

**Accepted:** 29 January 2021

**Published:** 08 March 2021

## Additional Files

### Add File 1. Interview conducted in each locality (Spanish version)

Encuesta realizada a los pobladores

Localidad:	Clave:	Fecha:
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1.- Datos del encuestado:

Nombre:

Edad:

Sexo:

Parentesco:

### IMPORTANCIA Y USOS

1. ¿Conoce las bromelias?
2. ¿Cuáles son las bromelias que usted conoce?

Nombre zapoteco	Significado Español	Parte utilizada Usos	Nombre Forófito Zapoteco	Significado Español	Parte utilizada Usos

¿Cuál es la más bonita?

¿Cuál es la que recolecta más? ¿Por qué?

Nombre	¿Dónde o a quién se la compra?	Precio

3. ¿Quién le enseñó a usted como se ocupan las bromelias?

### PERCEPCIÓN

4. Cuando sale a buscar bromelias ¿Ha notado que algunos tipos de bromelias ya no existen o que ya no hay tantas como antes?
5. ¿Por qué cree que ya no existan algunas bromelias o haya menos?

### RECOLECCIÓN

6. Cuando va a coleccionar bromelias, ¿Va usted solo o alguien lo acompaña?
7. ¿Cuáles son los lugares donde pueden recolectar bromelias?
8. ¿Desde hace cuánto tiempo va a recolectar? ¿Con quién aprendió a recolectar?

9. ¿Siempre ha recolectado las mismas bromelias o por qué ahora recolecta otras?
10. ¿Cada cuándo sale a recolectar bromelias?
11. ¿Cuánto tarda en llegar ahí y cuánto tiempo tarda en recolectar las bromelias?
12. Desde que usted empezó a recolectar ¿Invierte el mismo tiempo en llegar al sitio y recolectar las bromelias?
13. ¿Las bromelias que recolectan son de: árbol, suelo o de rocas?
14. ¿Utiliza alguna herramienta para recolectar las bromelias?
15. ¿Qué hace con las bromelias después de bajarla del árbol?
16. ¿Existen temporadas en las que se recolecten más bromelias? ¿Por qué?
17. ¿En qué árboles ha visto que crecen las bromelias?
18. ¿Utiliza la madera de los árboles para tener leña?
19. ¿Cuáles son los árboles que más utiliza para leña?
20. ¿Existe alguna organización con otras personas de su comunidad para recolectar las bromelias?
21. ¿Cree que las bromelias tienen alguna función en el bosque?
22. ¿Cree que sea necesario cuidar a las bromelias?
23. ¿Usted o su comunidad conocen alguna técnica o han tenido acciones para cuidar a las bromelias?
24. ¿Existen lugares dónde esté prohibido recolectar bromelias?
25. ¿Hay tipos de bromelias que estén prohibidas recolectarlas?
26. ¿Quién dice que está prohibido?
27. ¿Qué opina acerca de esas prohibiciones?

#### **VENTA**

28. ¿Quién va a vender las bromelias que usted recolecta?
29. ¿Dónde va a vender las bromelias?
30. ¿Por qué va a ese lugar?
31. ¿Existe algún procedimiento para que usted pueda vender las bromelias en ese lugar?
32. ¿Cuánto tiempo tarda en llegar a ese lugar?
33. ¿Utiliza algún transporte para llegar al lugar donde vende las bromelias?
34. Cuando llega a ese lugar para vender sus bromelias ¿Usted paga para poder venderlas?

Uso de suelo	Comida	Otros
Luz	Cuotas	

35. ¿Cuánto tiempo está en ese lugar para vender sus plantas?
36. ¿En qué meses vende más bromelias?
37. ¿En años anteriores usted vendía más bromelias o actualmente vende más?
38. ¿Cuántas bromelias vende en promedio en un día?
39. ¿Arregla de alguna manera a la bromelia para su venta?

**Add File 2.** Characteristics of sampling sites in San Juan Tabaá (SJT) and Santo Domingo Yojovi (SDY). Selection was based on the preference of bromeliads with greater cultural importance (BGCI), as well as the frequency of harvest activities developed by local inhabitants: Recurrent Harvest Site (RHS) and Occasional Harvest Site (OHS).

HARVEST FREQUENCY	LOCAL NAME OF SAMPLING SITE	DISTANCE FROM THE TOWN (Km)	ALTITUDE (m a.s.l.)	SLOPE	TYPE OF VEGETATION	MANAGEMENT HISTORY
Occasional Harvest Site (OHS)	<b>SJT</b>					
	Rhanshanashi	3.34	1 634	14° NO	Oak-Pine	50 years ago, all trees were cut down. Now, they are under natural growing.
	Sadao	3.55	1 543	55° SE	Oak	20 years ago, a fire devastated this area. Now, trees are growing naturally.
	Shagashi	3.66	1558	35° NE	Oak	30 years ago, all trees were cut down because people had authorization. Now, trees are growing naturally.
	<b>SDY</b>					
	Sinashino	3.01	1 437	15° NO	Pine-Oak	60 years ago, it was an oak forest, a fire disturbed this area, and now it grows oaks and pines.
	Yoyarhe	3.13	1 760	30° N	Oak-Pine	15 years ago, wood harvest was restricted. Now, they are under natural growing.
Recurrent Harvest Site (RHS)	Yanrhaá	2.49	1 935	25° NO	Oak-Pine	This area has maintained the same type of vegetation for the last 60 years, and now wood harvest is restricted.
	<b>SJT</b>					
	Achevieshé	3.88	1 562	30° NE	Pine-Oak	Wood harvest for fuel is authorized.
	Corrosoberry	4.56	1 714	5° SO	Pine-Oak	Wood harvest for fuel is authorized.
	Shasarua	3.03	1 631	20° O	Oak-Pine	50 years ago, a fire devastated this area. Now, wood harvest for fuel is authorized.
	<b>SDY</b>					
	Becoyo	2.76	1 711	5° SO	Pine	Wood harvest for fuel is authorized.
Yayasecuide	2.37	1 811	10° NE	Pine	Wood harvest for fuel is authorized.	
Yenshua	2.80	1 673	15° N	Pine	50 years ago, it was an oak forest, because the intensity of wood harvest, there are only pines.	



**Add File 3.** Tree structure in the sampling sites: Recurrent Harvest Site (RHS) and Occasional Harvest Site (OHS) in both localities: San Juan Tabaaá (SJT) and Santo Domingo Yojovi (SDY). *A*= Abundance, *RF*= Relative Frequency, *BA*= Basal Area; *RBA*= Relative Basal Area; *CV*= Canopy Volume and *RCV*= Relative Canopy Volume

		TREE SPECIES	<i>A</i>	<i>RF</i> (%)	<i>BA</i> (m <sup>2</sup> )	<i>RBA</i> (%)	<i>CV</i> (m <sup>3</sup> )	<i>RCV</i> (%)
SJT	OHS	<i>Quercus elliptica</i>	21	33.9	106.5	29.5	36307.9	62.4
		<i>Quercus obtusata</i>	13	21	71.4	19.8	6744.6	11.6
		<i>Quercus rugosa</i>	10	16.1	93.6	26	871.2	1.5
		<i>Quercus scytophylla</i>	7	11.3	35.6	9.9	10882.5	18.7
		<i>Phyllonoma laticuspis</i>	3	4.8	5.9	1.6	227.8	0.4
		<i>Gaultheria erecta</i>	3	4.8	6.8	1.9	122	0.2
		<i>Clethra occidentalis</i>	2	3.2	13	3.6	223	0.4
	<i>Vaccinium</i> aff. <i>leucanthum</i>	2	3.2	10.7	3	26.2	0.04	
	<i>Pinus chiapensis</i>	1	1.6	17	4.7	2812.7	4.8	
	<i>Pinus chiapensis</i>	15	35	151.8	48.9	103897.3	70.7	
	RHS	<i>Quercus obtusata</i>	11	25.6	83.9	27	22750.7	15.5
		<i>Quercus elliptica</i>	9	18.6	34	11	9221.7	6.3
		<i>Clethra occidentalis</i>	6	14	29.6	9.5	8824.5	6
		<i>Quercus rugosa</i>	3	7	11.1	3.6	2318.9	1.6
SDY	OHS	<i>Quercus elliptica</i>	43	53.8	132.2	42.8	91740.2	61.3
		<i>Quercus scytophylla</i>	7	8.8	110.4	35.7	49594.3	33.1
		<i>Pinus oocarpa</i>	22	27.5	42.7	13.8	4609.2	3.1
		<i>Agarista mexicana</i>	4	5	11.5	3.7	1893.9	1.3
	RHS	<i>Clethra occidentalis</i>	1	1.3	6.7	2.2	1534.4	1
		<i>Pinus chiapensis</i>	3	3.8	5.3	1.7	271.1	0.2
		<i>Pinus oocarpa</i>	13	65	87.9	65.9	21855	84.5
		<i>Pinus chiapensis</i>	6	30	44.7	33.5	3989.4	15.4
		<i>Clethra occidentalis</i>	1	5	0.8	0.6	17.7	0.1