Sustainable harvesting and conservation of *Laelia furfuracea*, a rare epiphytic orchid from Oaxaca, Mexico

Octavio Orozco-Ibarrola | Rodolfo Solano | Teresa Valverde

Abstract

Many epiphytic orchids are harvested in Mexico for different purposes. *Laelia furfuracea* is one of the most intensively traded species. Its inflorescences are used as ornaments during the December festivities. We investigated the effect of severing the flowering pseudobulb. This is the traditional technique frequently used by collectors at the study area. We wished to investigate its effects on the production of new pseudobulbs, as well as on their size and flowering probability. Also, we examined the survival probability and growth of individuals that had fallen on the ground to evaluate their potential as trading resources. Inflorescence collection did not affect the production of new pseudobulbs the following season. However, it affected the size of these pseudobulbs, as well as their flowering probability. Yet, the direction of this effect was not consistent between years. Nearly six percent of all *L. furfuracea* plants at the study site were found on the ground. Over 80 percent of them survived for at least two years, although most of them showed pseudobulb loss over that period of time. We conclude that harvesting of flowering pseudobulbs may be sustainable in terms of its effects on plant performance, at least in the short term. The active management of plants that have fallen on the ground may reduce the harvesting pressure on natural populations. Harvesting of flowering pseudobulbs may diminish some aspects of plant performance, but its effects need to be evaluated with complete life cycle data and take into account interannual variation in vital rates.

Keywords

endemic species, fallen epiphytes, inflorescence collection, non-timber forest products, pseudobulb survival

1 | INTRODUCTION

Many orchid species have been harvested in Mexico since pre-Columbian times. They are used for different purposes, such as ornamental, medicinal, ritual, and also as food, and as adhesives in artistic designs (Cruz-García, Lagunez-Rivera, Chavez-Angeles, & Solano-Gómez, 2015; Flores-Palacios & Valencia-Díaz, 2007; García-Peña & Peña, 1981; Hágsater, Soto, Salazar, Jiménez, López, & Dressler, 2005; Urbina, 1903). Whole plants, plant fragments, or inflorescences are extracted from their habitats to satisfy the demand of local markets, thus threatening the persistence of natural populations (Soto-Arenas, Solano-Gómez, & Hágsater, 2007).
out in different species and places are sustainable (Dutra-Elliott, 2014; Emeterio-Lara, 2019). The effects of harvest depend on the following factors, among others: (a) the nature of the harvest unit, that is, whole plants, plant fragments, or inflorescences (Mondragón, 2009); (b) the rate at which natural populations can regenerate the lost biomass (Emeterio-Lara, 2019); and (c) the frequency and intensity with which populations are harvested (Dutra-Elliott, 2014). In orchids, when the harvest units are plant fragments, population numbers are not necessarily affected in a direct manner. However, these fragments usually carry inflorescences. Thus, this form of harvest results in a reduced reproductive input of the affected plants. In addition, plant severing may result in a lowered growth rate or a decreased survival probability of the severed plants (Emeterio-Lara, 2019; Parra-Tabla, Vargas, Naval, Calvo, & Ollerton, 2011).

Irrespective of whether whole plants or plant fragments are the harvest unit, an additional aspect that remains to be investigated is the potential role of individuals that have fallen on the ground to satisfy at least some of the commercial demand for this type of plants. In another group of epiphytes, the bromeliads, it has been suggested that naturally fallen individuals, which may survive on the ground for up to 1.5 yr, could be a significant source of plant material whose exploitation may reduce the harvest pressure on natural populations (Mondragon & Ticktin, 2011; Toledo-Aceves, Hernández-Apolinar, & Valverde, 2014). In epiphytic orchids, this form of exploitation has also been reported and may play an important role in this respect (Cruz-García et al., 2015), allowing harvesters to take advantage of living plant material that otherwise would be lost over time. However, the length of time they can remain alive—and therefore potentially exploitable—on the ground is unknown.

In the Mexican state of Oaxaca, several epiphytic orchids are harvested and marketed. This region is exceptional for its high biodiversity, endemism, and cultural/ethnic richness (Ordoñez & Rodríguez-Hernández, 2008), and the Orchidaceae family is one of the most diverse, with 733 species reported (Salazar, 2012; Solano-Gómez, Martinez-Ovando, Martinez-Feria, & Gutiérrez-Caballero, 2016). Dutra-Elliott (2014) identified 19 orchid species being traded between March 2010 and April 2011 in the central market of Oaxaca city (the “Central de Abastos” in the state’s capital city). Of these, 35,790 specimens were Laelia furfuracea Lindl. pseudobulbs with inflorescence (Figure 1a). In a similar study, Cruz-García, Lagunez-Rivera, Chavez-Angeles, and Solano-Gómez (2015) recorded 36 orchid species being sold in the street markets of the village of Tlatlaxco, located in the western part of the state of Oaxaca. The latter study identified Laelia furfuracea as the most intensively traded species, with 7,834 items (whole plants, plant fragments, or inflorescences) being traded between October 2011 and January 2012, during its flowering months. Also, Molina-Luna, Arellanes-Cancino, and Martinez (2015) reported that L. furfuracea was the most intensively traded species (orchids and bromeliads considered) during the Christmas season in markets within the central region of Oaxaca. Ticktin et al. (2020) also identified L. furfuracea as one of the most important species of the orchid trade in Mexico.

The harvesting and commercialization of non-timber forest products (NTFP), which include orchids, are an important source of income for millions of people around the world (Schmidt, Mandle, Ticktin, & Gaoue, 2011). In the rural areas of many developing countries, family income is supplemented by the harvesting and trading of NTFP, which reduces poverty and supports livelihood diversification. As mentioned above, plants and inflorescences of L. furfuracea are important NTFP in Oaxaca. They are intensively extracted from their habitat and traded mostly in local traditional markets. Their use is mainly ornamental and ritual. In particular, temples and churches in many Oaxacan villages are adorned with L. furfuracea flowers during the December festivities (Cruz-García et al., 2015; Dutra-Elliott, 2014; Molina-Luna et al., 2015). One form of harvest is the extraction of whole plants from their natural populations.

FIGURE 1 (a) Laelia furfuracea plant in the field established on a Quercus sp. tree. (b) and (c) Example of pseudobulb severing practiced by plant collectors and applied in the “extraction” experiment in this study.
Alternatively, local people cut flowering pseudobulbs in half, removing the inflorescence, and leaving the rest of the plant behind (Cruz-García et al., 2015; Figure 1b,c). In the latter case, the two meristems located at the base of the pseudobulb are left intact, which allows the development of a new pseudobulb from which a new inflorescence may eventually grow (Cruz-García et al., 2015). This is the traditional technique commonly used to harvest L. furfuracea and other epiphytic orchids in the region (Cruz-García et al., 2015). Thus, although the extracted inflorescence is prevented from making a reproductive contribution to population growth, at least the harvested plant remains in its habitat, that is, its exploitation does not add to natural mortality, and it can make a reproductive contribution to population growth in future years through the production of new pseudobulbs.

The aim of this study was twofold: to investigate (a) how the severing of the flowering pseudobulb in L. furfuracea affects the production of new pseudobulbs, and how it impacts their flowering probability in the next growing season; and (b) whether fallen L. furfuracea plants are a realistic resource for pseudobulb and inflorescence harvest in terms of their probability of survival and growth in the short term (one or two years). It has previously been suggested that the intense harvesting pressure on L. furfuracea may be seriously depleting its natural populations (Acosta-Castellanos, 2002; Anonymous, 1991; Halbinger & Soto-Arenas, 1997). Thus, the knowledge about the response of individual plants to harvesting is an important step toward the design of sustainable harvesting regimes and conservation programs.

2 METHODS

2.1 The study species

Laelia furfuracea (Figure 1a) is known in the study region with the common names “lirio morado” (in Spanish), “gihtsl” (in the Mixtec language) or “ita ndeka morada” (in Mixtec-Spanish) (Halbinger & Soto-Arenas, 1997). It is a small epiphyte with clustered oblong-ovoid pseudobulbs. At the apex of each pseudobulb grows a single straight, rigid leaf. From the pseudobulb apex emerges a short raceme that bares 1–3 (exceptionally 4–5) rose to rose-pink flowers that are 7–9 cm wide (Figure 1a). These pleasantly scented flowers are produced from October to January and last for about 3 weeks (Halbinger & Soto-Arenas, 1997; and personal observation). Each plant (a group of pseudobulbs with a common genetic origin) may produce a single raceme (i.e., inflorescence) per season from the apex of the leading pseudobulb. Some plants may have several “growing fronts,” or leading pseudobulbs, and may thus produce several inflorescences in the same season.

Laelia furfuracea has been reported as endemic to the mountainous regions of the Mexican state of Oaxaca (Halbinger & Soto-Arenas, 1997; Solano, Huerta-Espinoza, Cruz-García, & Ortiz-Riveros, 2019). It is found in temperate forests situated in altitudes between 2,100 and 3,000 m a.s.l., within which it establishes mainly on some Quercus species (Q. castanea Née, Q. urbani Trel., and Q. liebmani Oerst. ex Trel.) (Halbinger & Soto-Arenas, 1997). This species is listed on the Mexican red list of endangered species (NOM-059-SEMARNAT-2010) under the category “subject to special protection” (Trujillo-Segura, 2019), due to the fact that it is exploited by local people. Some authors even consider it vulnerable or threatened because it is thought to be overexploited (Acosta-Castellanos, 2002; Anonymous, 1991). Here, we refer to it as “rare” due to its restricted geographic distribution and its high habitat specificity (Acosta-Castellanos, 2002; Halbinger & Soto-Arenas, 1997).

2.2 The study site

This study was carried out in the Mixteca region, within the Mexican state of Oaxaca (municipality of Santo Domingo Yanhuitlán, Nochixtlán district. Figure S1). The specific area where this research was conducted has been designated as a conservation site by the municipal authorities; thus, no NTFP extraction has been permitted since 2010 (although we believe there is some low-intensity extraction which is unlikely to have affected our experimental plants). The altitude at this site varies between 2,380 and 2,580 m a.s.l. The climate is temperate, subhumid, with the majority of the precipitation falling during the summer months (June to September) (INEGI, 2010). The mean annual rainfall is 420 mm, and the mean annual temperature is 16.9°C, with January being the coldest month (monthly mean: 6.5°C) and May being the warmest (monthly mean: 22°C) (Contreras-Hinojosa et al., 2005). The vegetation type is a seasonally dry temperate forest where the dominant tree species are Quercus liebmannii, Q. acutifolia Née, and Q. laurina Bonpl. (García-Mendoza, Tenorio, & Reyes, 1994). The geologic substrate is composed of extrusive igneous rocks, and soils are predominantly phaeezem type (INEGI, 2010).

2.3 Fieldwork

The study consisted of two sections: (a) inflorescence extraction and evaluation of subsequent growth and reproduction of the new pseudobulbs; and (b) survival and growth of the individuals that had fallen from host trees. For both sections, data were gathered in the flowering seasons of 2016, 2017, and 2018.

2.3.1 Inflorescence extraction

During December 2016, 70 flowering L. furfuracea plants were selected at the study site and allocated randomly to one of two treatments: control (N = 45) or extraction (N = 25). To locate the plants, we did random walks at the study site covering an altitudinal interval from 2,380 to 2,580 m a.s.l., and all the plants observed during these walks were included in the study (with the exception of those that were inaccessible or badly damaged by herbivory). All the plants were tagged and the number of live pseudobulbs was counted; the pseudobulb bearing the inflorescence was measured (length and diameter).
The extraction treatment consisted of the transversal severing of the pseudobulb with the inflorescence, in the same way, it is traditionally done for commercialization (Cruz-Garcia et al., 2015; Figure 1b and c). Control plants were left intact. In December 2017, both control and experimental plants were monitored to check whether they had produced a new pseudobulb (in which case it was measured), and whether these newly produced pseudobulbs had flowered.

In the same way, in December 2017, a different set of 75 flowering plants selected as described above were tagged and randomly allocated to one of two treatments (control, N = 45; and extraction, N = 30). They were followed up to December 2018, recording the same variables as previously described. With these data, we wished to evaluate the effect of the removal of the flowering pseudobulb on the probability of producing a new pseudobulb the following growing season, as well as on the size of the new pseudobulb, and its flowering probability.

2.3.2 | Survival and growth of fallen individuals

Between August 2016 and January 2017, random walks were carried out at the study site within the altitudinal interval from 2,380 to 2,580 m a.s.l.; 36 phorophytes (most of them Quercus liebmannii) bearing a considerable number of L. furfuracea plants were located during these walks. All L. furfuracea individuals established on these phorophytes, as well as all individuals that were found fallen on the ground below the canopy of these trees, were tagged, their number of live pseudobulbs counted, and the size of the largest pseudobulb measured (the largest pseudobulb is usually the youngest, that is, the one that represents most closely the current state of the plant). L. furfuracea plants store water and nutrients in their pseudobulbs, so pseudobulb number and size may be related to their survival probability and growth potential. In addition, the presence of inflorescences was noted. We had no information regarding the length of time these individuals had been on the ground, but they were alive at the moment of tagging. Individuals were allocated to one of five size-stage categories (Table 1). Two years later (between September 2018 and January 2019), individuals were relocated to check whether they were still alive, in which case their number of pseudobulbs was counted and the size of the largest pseudobulb measured.

2.4 | Statistical analyses

To evaluate the effect of extraction on the probability of plants producing a new pseudobulb, we used a generalized linear model (GLM) with a binomial error distribution, in which the dependent variable was the presence/absence of a new pseudobulb, and the independent—experimental—factors were treatment (extraction versus control) and year (2016 versus 2017). We were also interested in testing the significance of the interaction between these two factors, to explore whether the effect of extraction varied between years. In addition to the main experimental factors, we incorporated the number of pseudobulbs per plant and the diameter of the focal pseudobulb as covariates (the focal pseudobulb was the severed one, in the case of the extraction treatment; and the tagged one, in the case of the control).

In a similar manner, to evaluate the effect of extraction on the probability of new pseudobulbs flowering, we built an analogous GLM in which we took into account the plants that had produced a new pseudobulb, with the dependent variable being the presence/absence of an inflorescence, and the independent variables (with their corresponding interactions) being treatment (extraction versus control) and year (2016 versus 2017), incorporating as covariates the number of pseudobulbs per plant and the diameter of the focal pseudobulb. Also, to assess the effect of extraction on the size of the new pseudobulb, we built a linear model (with a normal error distribution) only with the plants that produced a new pseudobulb, with the dependent variable being the diameter of the new pseudobulb, and the independent variables (with their interactions and covariates) the same as before.

Regarding the fallen plants, we calculated the proportion of the total number of plants in each category (see Table 1 for category definition) that were found on their phorophytes and the proportion that were found on the ground. We built a GLM with a binomial error distribution, the dependent variable being survival, and the independent variables being position (on the ground or on the phorophyte) and number of pseudobulbs. Additionally, we estimated the growth of each individual as its number of pseudobulbs in 2018 minus its number of pseudobulbs in 2016, and we built an additional GLM with a Poisson error distribution (first testing for overdispersion and co-linearity) to test the effect on plant growth of category (with 4 levels, as no seedlings were found on the ground), position

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**TABLE 1** Size/stage categories used to classify the L. furfuracea individuals studied. The critical criterion to classify plants as R1 or R2 was the presence of inflorescences, its number of pseudobulbs being a secondary criterion to discriminate between the two, and the size of the largest pseudobulb being irrelevant for those categories.

| Category              | No. of pseudobulbs | Size (diameter) of the largest pseudobulb | Inflorescences |
|-----------------------|--------------------|------------------------------------------|---------------|
| Seedlings (S)         | 1-2                | <6.5 mm                                  | No            |
| Non-reproductive 1 (NR1) | 3 or more         | 6.6 to 12 mm                             | No            |
| Non-reproductive 2 (NR2) | 3 or more         | >12 mm                                   | No            |
| Reproductive 1 (R1)  | ≤100               | Yes                                      |               |
| Reproductive 2 (R2)  | >100               | Yes                                      |               |
(on the phorophyte versus on the ground), and the interaction between them, with initial number of pseudobulbs as a covariable. Generalized linear models were carried out in R (version 3.5.2).

3 | RESULTS

3.1 | Inflorescence extraction

Among the plants subjected to extraction, 70.8 and 64.3% of them (in 2016 and 2017, respectively) produced new pseudobulbs. Values were slightly lower among the control plants (64.3 and 51.2%; Table 2, Figure 2); however, the effects of treatment and year on the probability of producing a new pseudobulb were not significant, neither was the effect of the covariables (Table 3a).

From the plants that grew new pseudobulbs, 35.3 and 16.7% (in 2016 and 2017, respectively) produced inflorescences in the extraction treatment, whereas 14.8 and 42.9% did in the control (Table 2, Figure 2). In this case, the effect of treatment and year, as well as the interaction between them, was significant, while the covariable number of pseudobulbs and diameter of the focal pseudobulb before the start of the experiment were not significant (Table 3b).

The mean diameter of the new pseudobulbs produced the growing season following the start of the experiment was 15.1 and 15.4 cm in the extraction treatment (in 2016 and 2017, respectively) and 13.7 and 18.4 in the control (Table 2). Again, the effect of treatment, year, and the interaction between them was significant (Table 3c). Also, the diameter of the focal pseudobulb (which was introduced as a covariable) positively influenced the size of the new pseudobulb, while the number of pseudobulbs did not affect it (Table 3c).

3.2 | Survival and growth of fallen individuals

During our initial survey (August 2016 to January 2017), the category with the highest number of fallen individuals was R1, followed by NR1 and NR2 (see Table 1 for category definition). A very small number of R2 individuals (Reproductive 2, plants with more than 100 pseudobulbs) were found on the ground (Figure 3). Almost 6% of all the individuals counted in the survey area were found on the ground (Figure 3). It is worth remembering that the length of time these individuals had been on the ground is unknown.

The percentage of individuals surviving after two years was significantly higher among the plants established on phorophytes than in those fallen on the ground (Figure 4, Table 4). Also, the percentage surviving increased with plant size (i.e., survival was higher in larger categories, especially among fallen individuals; Figure 4). The effect of the number of pseudobulbs at the start of the survey on the probability of surviving to 2018–2019 was also significant (Table 4). For plants with a small number of pseudobulbs, survival probability was lower for individuals fallen on the ground than for those established on phorophytes (Figure 5).

Overall, plant growth (number of pseudobulbs in 2018 – number of pseudobulbs in 2016) tended to be higher among plants established on phorophytes than in those fallen on the ground for all plant categories (Figure 6). However, the effect of position (ground versus phorophyte) was not significant (Table 5). The effect of the number of pseudobulbs at the start of the observation period was significant (Table 5); plants with a larger number of pseudobulbs grew more slowly than those with fewer pseudobulbs. The interaction between position and category was significant mainly due to the fact that R1 plants (i.e., reproductive plants with < 100 pseudobulbs) lost a large number of pseudobulbs over time when they were on the ground (Table 5, Figure 6).

4 | DISCUSSION

Traditional harvest methods for L. furfuracea include the removal of flowering pseudobulbs. Those inflorescences are obviously prevented from making a contribution to the next seedling generation, either through the distribution of their pollen, or through seed production (pollen is ripe at the time of anthesis, but inflorescences are generally harvested just before anthesis). However, the plants they were harvested from are left behind and their survival is not affected (Cruz-Garcia et al., 2015), nor is their ability to produce new

| Table 2 | (a) Number (percentage) of plants producing new pseudobulbs; (b) number (percentage) of plants producing inflorescences, among those that produced a new pseudobulb; and (c) mean diameter (standard deviation) of the new pseudobulbs in different treatments (extraction and control) and years (2016 and 2017) |
|---------------------------|---------------------------------|-----------------------|-----------------------------|
| **Year/Treatment** | **N** | **(a) Plants producing new pseudobulbs (%)** | **(b) Pseudobulbs producing inflorescences (%)** | **c) Mean diameter of new pseudobulb (SD)** |
| 2016 Extraction | 24 | 17 (70.8) | 6 (35.3) | 15.1 (4.71) |
| Control | 42 | 27 (64.3) | 4 (14.8) | 13.66 (7.29) |
| 2017 Extraction | 28 | 18 (64.3) | 3 (16.7) | 15.4 (5.98) |
| Control | 41 | 21 (51.2) | 9 (42.9) | 18.44 (4.27) |

Although 70 and 75 individuals (for 2016 and 2017, respectively) were originally included in the experiment, some were lost due to herbivory and others were impossible to relocate.
pseudobulbs (Table 3). In fact, severed pseudobulbs were slightly more likely to produce new pseudobulbs compared to the controls (Table 2), although this effect was not significant. Thus, the traditional harvest method may be sustainable in this respect, or at least there is no evidence that harvest reduces the ability of the plant to produce new pseudobulbs, at least in the short term. This differs from what was observed in *L. autumnalis*, in which pseudobulb severing resulted in reduced plant growth, probably because *L. autumnalis* pseudobulbs are larger and their removal implies the loss of a higher proportion of biomass (Emeterio-Lara, 2019). Yet, it is necessary to carry out longer term experiments with *L. furfuracea* to observe the effect of prolonged harvest on the different components of plant performance. There is evidence in other NTFP that continued harvest of plant parts has cumulative detrimental effects on both plant performance and population growth rate (Gaoue, Horvitz, & Ticktin, 2011; Hernández-Barrios, Anten, & Martínez-Ramos, 2015; Nakazono, Bruna, & Mesquita, 2004; Valverde, Hernández-Apolinar, & Mendoza-Amaro, 2006).

The severing of flowering pseudobulbs had a significant effect on the probability of the new pseudobulb producing a new inflorescence. However, this effect depended on the year of observation (Table 4): pseudobulb severing in 2016 resulted in an increased flowering probability of the new pseudobulb, whereas the following year it caused a decrease (Table 2). It is important to note that both years were characterized by different weather conditions: plants subjected to extraction in 2016 actually experienced the weather conditions of 2017, during which rainfall was abundant (1,027 mm from May to October, Mixteca INIFAP meteorological station), whereas those subjected to extraction in 2017 experienced the weather conditions of 2018, which was a comparatively drier year (735 mm from May to October). We hypothesize that the relatively favorable conditions of 2017 allowed plants to compensate for the loss of biomass that resulted from pseudobulb extraction in 2016, while in the dryer year such compensation was not possible and pseudobulb extraction was detrimental. Thus, the prevalence of different weather conditions

![FIGURE 2](image-url) Percentage of plants that produced new pseudobulbs (left) and percentage of new pseudobulbs that produced an inflorescence (right) in the extraction and control treatment in 2016 and 2017

**TABLE 3** Results of the generalized linear model (GLM) used to test the effect of treatment (extraction versus control), and year (2016 and 2017) on the probability of producing a new pseudobulb in the following growing season. The original number of pseudobulbs and the diameter of the focal pseudobulb were used as covariables. (a) Results of the generalized linear model (GLM) used to test the effect of the factors and covariables on the probability of new pseudobulb production (residual's Shapiro–Wilk normality test: W = 0.988, p = 0.654). (b) Results of the linear model (LM) used to test the effect of the same factors and covariables on the diameter of the new pseudobulb.

| Model | Estimate | P     | CI (95%) | CI (95%) |
|-------|----------|-------|----------|----------|
| a) Probability of new pseudobulb production | Intercept | 1.172 | 0.241 | −0.075 3.400 |
|       | Treatment (control) | −299.6 | 0.845 | −330 2,710 |
|       | Year (2016) | −0.558 | 0.241 | −1.489 0.374 |
|       | No. pseudobulbs | −0.004 | 0.359 | −0.012 0.004 |
|       | Diameter | 0.042 | 0.397 | 0.039 0.139 |
| b) Probability of new pseudobulb flowering | Treatment × Year | 0.149 | 0.045 | −0.024 0.201 |
|       | Treatment | 0.042 | 0.972 | 0.029 0.054 |
|       | Year (2016) | −0.558 | 0.241 | −1.489 0.374 |
|       | No. pseudobulbs | −0.004 | 0.359 | −0.012 0.004 |
|       | Diameter | 0.042 | 0.397 | 0.039 0.139 |
| c) Diameter of new pseudobulb | Intercept | 4.950 | 0.017 | −9.390 9,880 |
|       | Treatment (control) | −299.6 | 0.845 | −330 2,710 |
|       | Year (2016) | −0.558 | 0.241 | −1.489 0.374 |
|       | No. pseudobulbs | −0.004 | 0.359 | −0.012 0.004 |
|       | Diameter | 0.042 | 0.397 | 0.039 0.139 |

Note: Significant effects are in bold numbers.
It is interesting that the size of new pseudobulbs behaved similarly to their probability of flowering: In 2016, severed plants produced larger pseudobulbs than control plants, whereas in 2017, the opposite pattern was observed (Table 2). It may well be that the two response variables are correlated and/or are affected by the same environmental factors, and thus, the smaller pseudobulbs produced in 2016 (in the control plants) had a lower flowering probability than the larger pseudobulbs produced in 2017, that is, the size of the pseudobulb may determine its ability to flower (Jacquemyn, Rein, & Jongejans, 2010; Pfeifer, Wolfgang, & Gottfried, 2006). Also, the effect of harvesting was similar on the two response variables, which suggests again that they may be correlated. This shows the importance of yearly environmental variation as a crucial driver of the behavior of the harvested individuals and points to the difficulty in setting standard quotas of inflorescence extraction. If harvesting promotes large new pseudobulbs and increased flowering probability in one year, but exactly the opposite the following year, it is difficult to come up with clear, unequivocal advice as to how best to exploit this species. Only a longer term experiment would provide the information necessary to understand this phenomenon in more detail.

In addition, the effect of harvesting and yearly environmental variation on pseudobulb size and flowering probability may also reflect on the different components of population dynamics. An evaluation of individual performance, as essential as it is, is no substitute for the type of information that may be derived from a detailed demographic analysis, which may show how population numbers respond to harvesting in the long run. There are only a few examples of population dynamics studies on epiphytic orchids in the literature and even less that evaluate the demographic effect of harvesting. Raventós, González, Mújica, and Doak (2015) worked with Dendrophyllax lindenii (Lindl.) Benth. ex Rolfe in Cuba and showed that the population is declining, in this case not due to overexploitation, but to increased hurricane frequency associated with climate change. Dutra-Elliott (2014) studied three populations of Prosthechea karwinskii (Mart.) J.M.H. Shaw in Oaxaca, México, and found that two of them are declining, most likely due to pseudobulb and whole-plant extraction. Mondragón (2009) used a demographic model to evaluate the effect of whole-plant harvesting on the population dynamics of Guaraniathe aaurantiaca (Bateman ex Lindley) Dressler & W.E. Higgins and estimated that even low levels of exploitation would result in population decline. This supports our suggestion that whole-plant extraction is indeed more detrimental compared to pseudobulb harvest, which is also a conclusion reached by other authors (Ticktin et al., 2020). Emeterio-Lara (2019) worked with Laelia autumnalis (La Llave & Lex.) Lindl. and found that population growth rate ($\lambda$) decreased as pseudobulb extraction increased. However, in the demographic analysis carried out by Hernández-Apolinar (1992) for Laelia speciosa (Kunth) Schltr., in which the units extracted were pseudobulbs with inflorescences, harvesting turned out to be sustainable. So whether harvesting involves the elimination of whole plants, or just a decrease in plant size, or a lowered contribution to fecundity, is likely crucial in relation to its demographic effects.

For epiphytic plants that are important NTFPs, it has been suggested that exploiting individuals that have fallen to the ground may be an alternative to active harvesting from standing populations.
The results of our study indicate that *L. furfuracea* plants may survive on the ground for at least two years, which suggests that they could potentially satisfy some of the commercial demand for this type of plants, although it is important to take into account that when they are on the ground, they are more prone to damage and their commercial value may decrease as a result. Additionally, fallen individuals lost pseudobulbs over time, whereas the plants established on phorophytes tended to gain pseudobulbs between 2016 and 2018 (Figure 6). This suggests that fallen individuals were in the process of dying, which may take over two years. As we do not know for how long these fallen individuals had been on the ground prior to our observations, we believe it is possible that they may remain alive on the ground for several years. This differs from what Mondragon and Ticktin (2011) found for the bromeliads *Tillandsia macdougallii* L.B. Sm and *T. violaceae* Baker, which died within 1.5 yr after falling to the ground. It is important to take into account, though, that bromeliads do not have long-term survival structures, such as orchid pseudobulbs.

**TABLE 5** Results of the generalized linear model (GLM) used to test the effect on plant growth (final number of pseudobulbs – initial number of pseudobulbs) of position (on phorophyte versus on the ground), and number of pseudobulbs at the start of the observation period in plants of different categories

|                          | Estimate | P       | Confidence interval (95%) |
|--------------------------|----------|---------|---------------------------|
| Intercept                | 4.616    | <0.0001 | 4.604 4.627               |
| No. Pseudobulbs          | −0.0012  | <0.0001 | −0.0017 −0.0006           |
| Position (ground)        | −0.024   | 0.270   | −0.067 0.018              |
| Category (NR2)           | 0.013    | 0.131   | −0.004 0.030              |
| Category (R1)            | 0.038    | 0.001   | 0.015 0.061               |
| Category (R2)            | 0.049    | 0.372   | −0.059 0.155              |
| Category (NR2) × Position (ground) | −0.049 | 0.148   | −0.116 0.017              |
| Category (R1) × Position (ground) | −0.133 | <0.0001 | −0.191 −0.075            |
| Category (R2) × Position (ground) | 0.047  | 0.539   | −0.104 0.197              |

Note: Significant effects are in bold numbers.

**FIGURE 5** Survival probability of plants established on phorophytes (gray circles) and fallen on the ground (black triangles), according to their number of pseudobulbs. Trend lines are the functions resulting from the GLM performed.

**FIGURE 6** Mean growth of plants in different size categories established on phorophytes (black) and fallen on the ground (gray). Growth is given in terms of the difference in the number of pseudobulbs in 2018–2019 with respect to 2016–2017. Error bars are standard deviations. Size categories as defined in Table 1. Sample sizes are on phorophytes, NR1 = 308, NR2 = 227, R1 = 206, R2 = 6; on the ground, NR1 = 17, NR2 = 11, R1 = 25, R2 = 3.
In the Mixteca region, it is known that local people collect fallen L. furfuracea individuals and cultivate them in their backyards to eventually use or sell their inflorescences (Cruz-García et al., 2015). We suggest this ex situ management does not affect population density, given that fallen individuals, although capable of remaining alive on the ground for a number of years, most likely do not make a contribution to population numbers. Although we did observe some fallen individuals produce ripe fruits, we estimate that the probability of the resulting seeds dispersing and arriving at microsites adequate for germination and establishment is low.

In conclusion, inflorescence collection in L. furfuracea may be sustainable when carried out through pseudobulb severing, at least in terms of its effects on plant survival and growth after one year. However, the harvesting of inflorescences does affect further inflorescence production, as well as the size of new pseudobulbs, although the direction of this effect is not consistent between years. Nearly six percent of all L. furfuracea plants found at the study site were on the ground. The probability of these plants surviving for at least two years is high and increases with plant size, although they tend to lose pseudobulbs over time.

We conclude that in addition to the results we present on individual plant performance in response to harvesting, it is necessary to carry out detailed demographic analyses to investigate the effect of exploitation and other aspects of management on population numbers. Notwithstanding, our results add significantly to the knowledge of epiphytic orchids subject to management and offer important insights that may aid in their conservation.

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DISCLOSURE
The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rn8pk0p71 (Orozco-Ibarrola et al., 2020).

ORCID
Teresa Valverde https://orcid.org/0000-0002-2008-8316

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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