Do epiphytes affect the fitness of their phorophytes? The case of *Tillandsia recurvata* on *Bursera copallifera*

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Abstract

The studies about the negative effect of epiphytes on their phorophytes show contradictory results and are based on limited variables (e.g., shoot survival). On branches of *Bursera copallifera,* we experimented with the transplantation/removal of *Tillandsia recurvata* and artificial tussocks, measuring shoot survival, growth, generation of new shoots, and production of inflorescences and fruits. Most single traits did not differ between treatments. The generation of new shoots was lower in the treatments where *T. recurvata* was present and increased in the branches where it was removed. The lowest shoot survival was in the treatments where *T. recurvata* was present or was removed. Removing *T. recurvata* increased plant relative fitness, and it was 43% lower in branches with *T. recurvata*. *Tillandsia recurvata* is a structural parasite of *B. copallifera*. A negative effect of epiphytes on their phorophytes appears counterintuitive since it would not be evolutionarily stable for an epiphyte to shorten the lifespan of its support. *Tillandsia recurvata* populations are concentrated on *B. copallifera* branches between 2-4 cm in diameter, while smaller branches are mostly empty, so it is possible that the negative effect of *T. recurvata* occurs in the smallest branches, explaining why *T. recurvata* populations are biased to larger branches.

Introduction

Interspecific interactions are among the most critical processes generating adaptation and variation in species (Thompson 1988). The different types of interactions are defined by the net fitness cost that interacting species assume (Forsman et al. 2002). True epiphytic plants (holoepiphytes) spend their entire lives on a phorophyte without contact with the floor and no development of a haustorium (i.e., parasitic 'roots', Benzing 1990). Few experimental studies have explored the mutual effects of the epiphyte-phorophyte interaction (Ruinen 1953, Flores-Palacios et al. 2014, Soria et al. 2014, Flores-Palacios 2016) or interactions among epiphytes (e.g., Victoriano-Romero et al. 2023). In some tree species, specific individuals or branches with a high load of epiphytes often present dead parts, which has led to the suggestion that the epiphytes 'parasitize' their phorophytes. For this reason, epiphytes have been called 'structural parasites' or 'nutrient pirates' and have even been considered weeds (Benzing and Seemann 1978, Benzing 1990, Bartoli et al. 1993, Montaña et al. 1997).

Based on observational evidence, six damage mechanisms of the epiphytes towards their phorophytes have been proposed: 1) mechanical damage due to weight (Benzing 1990, Bartoli et al. 1993, Montaña et al. 1997) or increasing the impact of strong winds (Einzmann et al. 2022), 2) epiphytosis (the negative effect of an epiphyte on its phorophyte exerted through the mycorrhizal fungus of the epiphyte roots, Ruinen 1953), 3) twig strangling and hypertrophy (Ruinen 1953; Benzing and Seemann 1978, Páez-Gerardo et al. 2005, Aguilar-Rodríguez et al. 2007, 2016, Pérez-Noyola et al. 2021), 4) the release of allelopathic substances that eliminate the leaves of the phorophyte to increase the light available to the epiphyte (light competition hypothesis, Benzing and Seemann 1978), 5) nutrient piracy (the epiphytes intercept leaves that would otherwise have been integrated into the soil leaf litter, thus interrupting nutrient cycles and impoverishing the soil, Benzing and Seemann 1978); and 6) shading (Montaña et al.1997, Flores-Palacios 2016).

Some of the authors who have suggested that epiphytes negatively affect their phorophytes (e.g., Benzing 1990, Flores-Palacios 2016) have nevertheless recognized that the epiphytes may not cause the association of dead branches with large epiphyte loads. The previous association could be a product of the trees' ontogeny and the epiphyte colonization rate. That is, old branches naturally die (i.e., self-pruning) and were also exposed to epiphyte colonization for an

extended time. This 'self-pruning hypothesis' could explain why experimental evidence failed to demonstrate the effects of epiphytes on their phorophytes (Flores-Palacios 2016).

Some experimental work suggests indirect damage mechanisms occur when the epiphytes fall to the ground (Flores-Palacios et al. 2014). Another line of evidence indicates that the presence of epiphytes in the trees is beneficial since they can: buffer the temperature (Stuntz et al. 2002, Stanton et al. 2014), provide nutrients and water (Gotsch et al. 2016) which can be taken up by the phorophyte through canopy roots (Nadkarni 1981). However, studies examining the effect of epiphytes on their phorophytes quantified only one phorophyte trait, and the combined effects of epiphytes on multiple traits have yet to be explored.

In this study, we determined experimentally whether the epiphyte *Tillandsia recurvata* (L.) L (Bromeliaceae) affects several fitness traits of its phorophyte *Bursera copallifera* (Kunth) Engl. (Burseraceae). We hypothesize that if *T. recurvata* is a structural parasite of *B. copallifera*, the branches colonized by this epiphyte, or those on which it has been transplanted, will present reduced vigour, and the attributes of fitness of the tree will diminish. In contrast, non-colonized branches, or those from which this epiphyte has been removed, will have greater vigour, and the attributes of fitness of the tree will be maintained or increased. However, suppose *T. recurvata* is a commensal of *B. copallifera*; in that case, the tree's vigour will be similar between branches colonized and not colonized by *T. recurvata* and between those where this epiphyte has been removed or transplanted. In addition to measuring individual phorophyte traits, we analysed the combined effects of various traits (including fruit production) on the relative fitness of *B. copallifera*.

Material and methods

Study site

The study was conducted in the tropical dry forest of the Cerro de la Cal, in San Andrés de la Cal, Tepoztlán, Morelos, central Mexico (18°57'22.2"N, 99°06'50.2" W). The elevation ranged from 1480 to 1670 m a.s.l. The annual average temperature is 18°C, and the mean yearly rainfall ranges from 800 to 1000 mm (Comisión Nacional del Agua, unpublished data). In the study area, the tropical dry forest harbours 19 species of vascular epiphytes; the most abundant holoepiphytic species are *Tillandsia recurvata* (76.7% of epiphyte individuals), *T. achyrostachys* E. Morren ex Baker (12.4%), *T. hubertiana* Matuda (2.7%), and *T. caput-medusae* E. Morren (2.5%) (Vergara-Torres et al. 2010). The dominant woody species include the endangered species *Sapium macrocarpum* Müll. Arg. (18.4% of individuals, Euphorbiaceae), *Bursera fagaroides* (Kunth) Engl. (14.8%), *B. glabrifolia* (Kunt) Engl. (11.0%), and *Conzattia multiflora* (B. L. Rob.) Standl. (6.5%, Fabaceae), which together account for 51.3% of the total number of individuals in the forest (Vergara-Torres et al. 2010). In the study area, *Bursera copallifera* (2.6% of the tree individuals) hosted 11.5% of the epiphyte individuals (Vergara-Torres et al. 2010).

The experiment of removal/transplantation of T. recurvata

Twenty *Bursera copallifera* trees were selected that appeared healthy, without any dry and dead sections (Figure 1). The average distance between trees was 141 ± 101 m (from now on, we report mean ± SD), with a minimum of 5 m and a maximum of 407 m. We accessed the tree crowns with a 6 m ladder and employed climbing gear for safety.

From each tree (Figure S1 in supplementary material), three sibling branches (originating from the same bifurcation or same branch) without *Tillandsia recurvata* were chosen, along with three sibling branches with *T. recurvata*. Every shoot on each branch was marked with an aluminium label. A shoot is considered the most distal twig of the branch, and it bears leaves and inflorescences (Flores-Palacios 2016). Each experimental branch was randomly assigned (with random numbers, Zar 2010) to one experimental treatment; the three branches without epiphytes were assigned to one of three treatments of epiphyte transplantation (see below); and the branches with epiphytes were raffled in three treatments of epiphyte removal (see below, Figure S1 in supplementary material). The branches used were of similar diameter (general mixed-effects model, F = 1.6, d. f. = 5, 95; P = 0.18; see Tables S1, S2 in supplementary material), had the same number of shoots (Poisson mixed-effects generalized model, $\chi^2 = 0.5$, d. f. = 5, P = 0.99; see Tables S1, S2 in supplementary material), and those with *T. recurvata* had 3 ± 2 tussocks (13% had one tussock, 50% had two tussocks, maximum = 8 tussocks). A tussock is a *T. recurvata* spheroid separate from any other spheroid (Flores-Palacios 2016).

One of the branches without epiphytes was selected randomly, and four adult *T. recurvata* tussocks were transplanted onto the branch (Transplanted Figure S1 in supplementary material). These epiphyte tussocks had old inflorescences and a 12-14 cm diameter. The second branch was left unmodified (control without epiphytes). At the same time, four artificial tussocks were placed on the third branch to simulate the effect of the weight and shade of *T. recurvata* (Artificial tussocks). The artificial tussocks were made of ixtle fibre because this material is, like *T. recurvata*, low in weight and allows light and air to pass through. One of the branches with *T. recurvata* was selected at random, and all epiphytes were eliminated (Removed); the second was not modified (Not removed). All epiphytes were eliminated from the third branch and then reattached (Removed/replanted) to control for the effect of removal. As done in previous works (e.g., Flores-Palacios 2016), all transplanted tussocks were fixed to branches with plastic straps.

The measures of performance we took were shoot survival, growth of shoots in length, and generation of new shoots on the branch, as well as production of inflorescences, and fruits, which were recorded monthly for 17 months. A shoot was considered dead when it no longer increased in length, was dry and without leaves, and considered alive when it had leaves and/or inflorescences/fruits, was green in colour at the tip and/or increased in length. New shoots that appeared over the observation period were marked and incorporated into the survival monitoring regime.

To determine whether there were differences among treatments in terms of the growth of shoots on the branches, the length of each shoot was measured at the end of the observation period by placing a ruler where the shoot meets the branch and recording the maximum length from that point to the apical tip of the shoot, disregarding the leaves. To standardize the measurements of shoot growth, the relative growth rate (RGR) of each shoot was calculated using the following formula:

$$RGR = \frac{L_{final} - L_{initial}}{L_{initial}}$$

The L_{final} is the length of the shoot at the end of the experiment, and $L_{initial}$ is the initial length of each shoot. The value RGR is equal to 0 if there is no growth and >0 if there is some growth. Usually, a
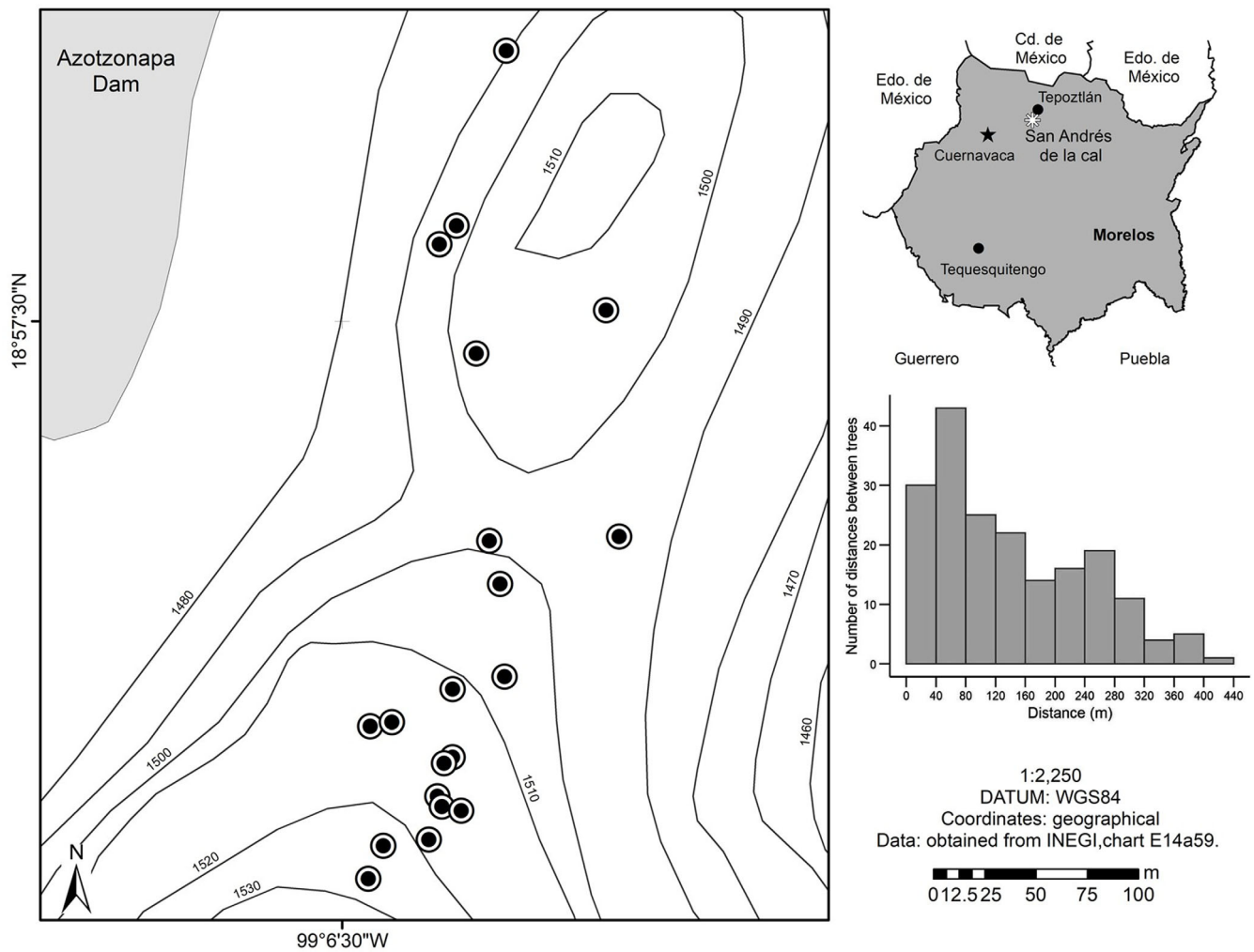
Figure 1. Distribution of *Bursera copallifera* trees used in an experiment to test the effect of *Tillandsia recurvata* on them. The field experiment was performed in the tropical dry forest of San Andres de la Cal, Morelos, Mexico. The histogram displays the distribution of distances between the 20 trees.

relative growth rate is preferred because this controls the effect of initial shoot size (Zotz 1998).

The effect of the treatments on the reproductive success of *B. copallifera* was measured with the number of inflorescences and fruits. The number of inflorescences (May - July) and fruits (June, when these began to be produced) on each shoot were quantified during the reproduction seasons 2010 and 2011.

Data analyses

All analyses were done in R 4.2.1 (R Core Team 2022), with the libraries ggplot2 for graphs (Wickham 2016), Summarytools for descriptive statistics (Comtois 2022), and those cited below. A survival analysis was conducted to test the effects of the treatments on the survival of shoots (Table S1 in supplementary material). This analysis measures the frequency of individuals that lived or died and the time that elapsed until the event of interest occurred (Kleinbaum and Klein 2005). Shoot survival between the treatments was compared using a log-rank test (Kleinbaum and Klein 2005). As the log-rank test revealed an effect of the treatments in the survival curves, we performed paired log-rank tests with the P value corrected for multiple comparisons (Bonferroni correction, Kassambara et al. 2021). Survival analysis

was done with the libraries survival for log-rank test (Therneau 2022) and survminer for multiple comparison and graphs (Kassambara et al. 2021).

In order to compare whether the emergence of new shoots differed between treatments, a χ^2 test of the accumulated frequency of the shoots was conducted (Zar 2010). A Haberman residuals test was used to determine which treatments had an abundance of new shoots that were higher or lower than that expected by chance (Haberman 1973, Siegel and Castellan 2005) (Table S1 in supplementary material).

To test if there were differences among treatments for the variables shoot growth, production inflorescences, and fruits, we used general linear or linearized mixed-effects models because our experimental design followed the design of a randomized block analysis of variance (Zar 2010) (Table S1 in supplementary material). In this model, all the possible treatments (fixed factor) are presented in each block (i.e., each tree, the random factor) and assigned randomly to the experimental units (branches inside the tree, Zar 2010). Branches were lost over the course of the experiment, and consequently, for some response variables, we used fewer trees (blocks) in the analysis. Because in some branches, the number of shoots was low (n=2), we did not include the effect of each branch in the mixed-effects model. In order to obtain only

Table 1. Initial total number of shoots, new shoots, and percentage of shoot survival of *Bursera copallifera* branches subjected to six treatments of removal/transplantation of epiphytes

Treatment	Initial shoot number	Number of trees with new shoots	Number of new shoots	Shoot survival
Not removed	123	5	8 (-7.3)	31 % [c]
Removed	134	10	**24** (8.7)	33 % [bc]
Removed and replanted	115	5	6 (-9.3)	46 % [ab]
Without epiphytes	116	11	18 (2.7)	49 % [a]
Transplanted	113	8	18 (2.7)	56 % [a]
Artificial tussocks	120	11	18 (2.7)	57 % [a]

Note: The treatments are presented in descending order of percentage of shoot survival (after 510 days of monitoring). For the new shoots, observed values lower than expected are presented underlined, and values higher than expected are presented in bold. The differences between observed and expected new shoots are shown in parentheses. In shoot survival, different letters correspond to different survival percentages (P < 0.05, Log-rank test adjusted for multiple comparisons).

one value for those response variables measured per shoot within the branches (RGR, number of inflorescences, and fruits), the total number of observations per branch was averaged. Mixed-effects models were done using the library lme4 (Bates et al. 2015). Similar mixed-effects models were done to compare the initial values of the branches (diameter) and the number of shoots, but for the later variable, we used a generalized mixed-effects model for a Poisson variable (Tables S1, S2 in supplementary material).

Based on the results of the previous analyses, a model was generated to calculate relative fitness in the *B. copallifera* branches subjected to different treatments (Table S1 in supplementary material). In this model, the destiny of a hypothetical cohort of 100 shoots was followed, considering the following events: generation of new shoots, survival of shoots, and production of fruits. Transition probabilities between events were taken from previous analyses. The value of each transition was averaged among treatments that did not differ significantly from each other (e.g., survival), and transition values were only left where previous analyses had shown them to be different. In the case of the production of new shoots, the ratios between the number of new shoots and the original number of shoots were used as the transition. These ratios were multiplied by the hypothetical cohort (resulting in the hypothetical number of new shoots) and then summed with the hypothetical cohort. We used the general mean value of fruits produced between the treatments and years for fruit production. Relative fitness ($\hat{w}$) in each treatment was calculated as the ratio between the estimated number of fruits (= reproductive success) in the shoots of each treatment and the maximum estimated number of fruits among treatments.

Results

After 510 days of observation, total shoot mortality was 55% (Table 1). Mortality was even observed among the new shoots, and the average lifespan of the shoots was 257 ± 157 days. Shoot survival differed among treatments (Log-rank test, $\chi^2 = 42.9$; d.f. = 5; P < 0.0001, Table 1). The lowest shoot survival occurred in the branches with epiphytes not removed and epiphytes removed

(Figure 2). In contrast, the highest shoot survival occurred in the branches where there were no epiphytes or in those where tussocks of *T. recurvata* or artificial tussocks had been transplanted (Figure 2). Shoot survival was intermediate among those groups of branches where the epiphytes were removed and replanted (Figure 2).

In general, shoot growth ranged from 0.1 cm to 13.9 cm (0.8 ± 1.4 cm, see Table S2 in supplementary material), and no differences were found in the relative growth rate of the shoots among treatments (F = 0.74; d.f. = 5,95; P = 0.60; Table S2). Few new shoots were generated on the branches (Table 1); only 92 shoots were observed among the six treatments, and 58% of the branches did not produce shoots after more than a year of observation (Table 1). Significant differences were observed in the number of new shoots ($\chi^2 = 15.5$; d.f. = 5; P = 0.01) among treatments (Table 1). In the epiphyte removal treatment, there were more shoots than expected (Haberman residual = 2.2), while in the removed and replanted treatment, there were fewer (Haberman residual = −2.4), a similar not significant tendency was observed in the removal treatment (Haberman residual = −1.9) (Table 1).

There was no difference in the number of inflorescences per shoot during the first ($\chi^2 = 2.01$; d.f. 5, P = 0.85) and the second season ($\chi^2 = 1.75$; d.f. = 5, P = 0.88) (see Table S3 in supplementary material). The same occurred with the number of fruits per shoot, and this number was similar between treatments in 2010 ($\chi^2 = 4.10$; d.f. = 5, P = 0.54) and 2011 ($\chi^2 = 2.75$; d.f. = 5, P = 0.74) (Table S3), even when we did not observe fruits in the treatments with epiphytes (Not removed, Removed and replanted, Transplanted) or in the branches with epiphytes removed (Table S3). The general (all treatments in both seasons) mean number of fruits per shoot is 3.3 ± 5.1.

The combined events suggest that if a cohort of shoots of the same size is compared among treatments, the branches with epiphytes will present the lowest relative fitness (Figure 3). Relative fitness will increase in branches subject to epiphytes removal (removed and removed/replanted) (Figure 3). The greatest relative fitness will be observed in branches free of epiphytes or those where epiphytes or artificial tussocks are placed (Figure 3).
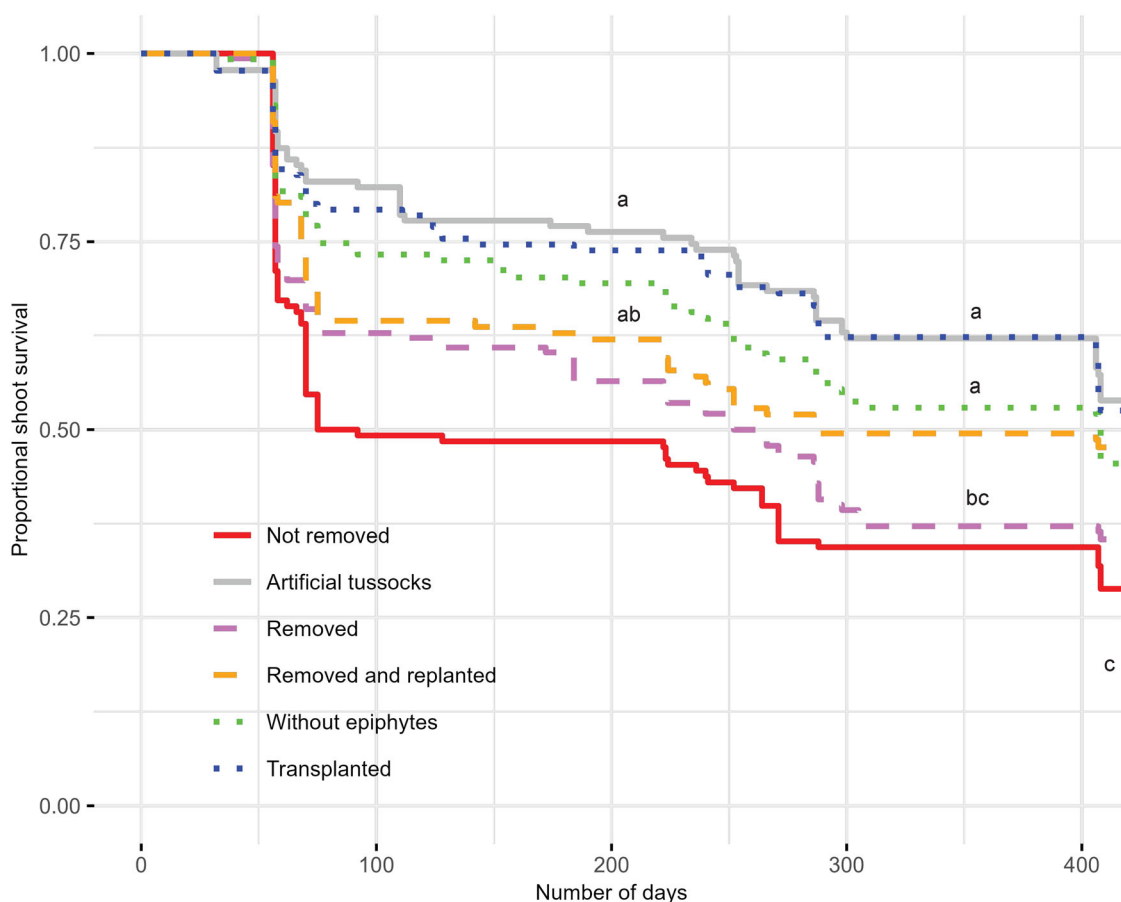
Figure 2. Survivorship of *Bursera copallifera* shoots over time on branches where the presence of *Tillandsia recurvata* tussocks was manipulated. Treatments were: *T. recurvata* tussocks either present but then removed (Removed), not removed, removed and replanted, absent but then transplanted (Transplanted), absent and not transplanted (Without epiphytes), and epiphytes absent but with artificial tussocks installed. Different letters indicate significant differences between the survival curves (Log-rank tests with the P values corrected for multiple comparisons, $P < 0.05$).

Discussion

This study tested whether an epiphytic species (*Tillandsia recurvata*) causes damage to the phorophyte (*Bursera copallifera*) on which the population of the epiphyte is concentrated in a tropical dry forest of Mexico (Vergara-Torres et al. 2010). The general hypothesis was that if *T. recurvata* acts as a structural parasite of *B. copallifera*, then attributes of fitness (e.g., shoot survival, production of inflorescences, fruits) will be lower in colonized branches or in those onto which *T. recurvata* is transplanted, but higher in those from which this epiphyte is removed or which were always free of the epiphyte. Most of the individual traits analysed in this experiment indicate that *T. recurvata* is a commensal of *B. copallifera*, discounting some damage mechanisms. However, two traits (shoot survival and generation of new shoots) indicate that *T. recurvata* has a relationship of structural parasitism with *B. copallifera*, and these traits affect the relative fitness of the branches with epiphytes.

It has been suggested that the shading and weight of the bromeliads damage the phorophyte (Benzing and Seemann 1978, Flores-Palacios 2016; Einzmann et al. 2022). We imitated this mechanism (artificial tussocks) and found no evidence of damage, suggesting that neither the weight nor shading of *T. recurvata* is causing damage to the branches. Shading caused by epiphytes can be beneficial for the trees (lowering the temperature and increasing the humidity; Stanton et al. 2014), but for green bark trees, shade

can have a negative effect on the branches if the coverage of epiphytes is high (Flores-Palacios 2016). Epiphytism in the study area (Vergara-Torres et al. 2010) is scarce and does not reach the levels seen in other forests where large tank *Tillandsia* species dominate, or *T. recurvata* is much more abundant. For example, in some semiarid ecosystems, *T. recurvata* colonizes all the available phorophyte species and reaches biomass values of up to 491.9 ± 92.3 kg/ha (Flores-Palacios et al. 2015), so it could be that heavy loads of epiphytes do not operate in the study area. The lack of impact of the artificial tussocks strongly suggests that the observed effects of *T. recurvata* on *B. copallifera* are not caused by its weight or shade.

It has been proposed that survival and growth of shoots are lower in branches infested with epiphytic plants (Ruinen 1953, Montaña et al. 1997; Flores-Palacios 2016). Our results suggest that shoot survival is affected by T. *recurvata* since the lowest survival was recorded in the branches where the epiphyte was not removed. However, the results of shoot survival were contradictory. Although we expected a decrease in shoot survival in the transplanted epiphytes treatment, it showed high survival. Moreover, the branches where *T. recurvata* was removed did not show any recovery in shoot survival. These data suggest that the removal of *T. recurvata* did not immediately resolve the effect of the epiphyte or that the trend of shoot mortality is independent of the presence of *T. recurvata*. This supports similar experimental
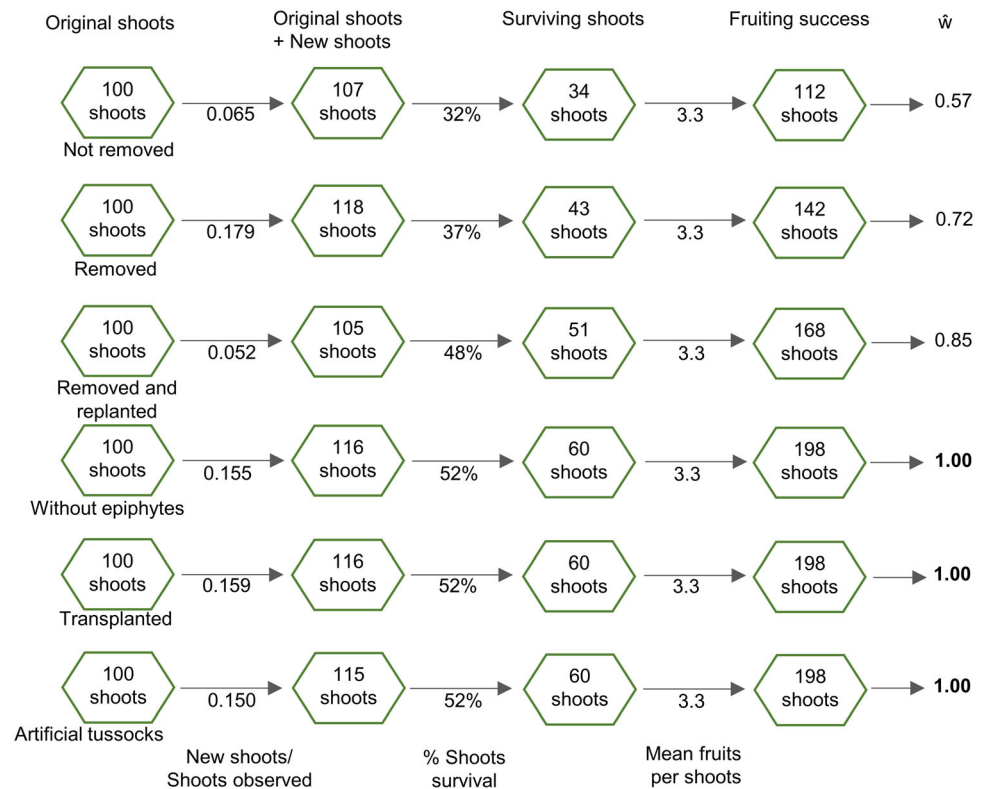
Figure 3. A schematic representation of the relative fitness (ŵ) consequences in *Bursera copallifera* caused by the presence of *T. recurvata*. Relative fitness was estimated by modelling the fruit production of a hypothetical shoot cohort (size 0 100) in six presence/absence treatments of *T. recurvata* and considering the average number of new shoots growing from the cohort, shoot survival, and fruit production. Treatments are: *T. recurvata* tussocks were either present but then removed (Removed), not removed, removed and replanted, absent but transplanted (Transplanted), absent and not transplanted (Without epiphytes), and absent but with artificial tussocks installed. At the bottom of the figure, and in line with the arrows, are the names of the transition values, while at the top of the boxes are the names of each trait and the relative fitness value (ŵ). For each treatment, relative fitness was estimated as the ratio between the number of fruits in the treatment and the maximum number of fruits.

evidence, where treatments of removal and transplantation of *T. recurvata* did not affect the dynamic of shoot survival in *Parkinsonia praecox* (Ruiz & Pavón) Hawkins (Fabaceae) (Flores-Palacios 2016). It is likely that in the treatment of removal and replanting of *T. recurvata*, the negative effect of the epiphyte was removed, and, on replacement of the epiphyte, its positive effect (shade, buffering of temperature, Stanton et al. 2014) contributed to a greater shoot survival.

Shoot growth was measured in two ways (relative growth rate and generating new shoots). Relative growth rate was unaffected by the presence of epiphytes, but, in agreement with the hypothesis of structural parasitism (Montaña et al. 1997), the branches from which the epiphytes were removed presented an increased generation of shoots, while the branches on which the epiphytes were maintained presented a lower generation of shoots. Benzing (1990) proposed allelopathogenic or strangulation mechanisms, which could cause hypertrophy (Páez-Gerardo et al. 2005, Aguilar-Rodríguez *et al.* 2007). Hypertrophy, associated with water scarcity in dry zones, could cause a reduction in the flow of water to the leaves (Aguilar-Rodríguez et al. 2007, 2016, Pérez-Noyola et al. 2021). It is possible that through hypertrophy, *T. recurvata* lowers the generation of new shoots in *B. copallifera*. The evidence about hypertrophy caused by *T. recurvata* is contradictory; some observational evidence exists for *Parkinsonia praecox* (Páez-Gerardo et al. 2005, Aguilar-Rodríguez et al. 2016), *Prosopis laevigata* (Humb. & Bonpl. Ex. Willd) M. C. Jonhst. (Fabaceae) (Aguilar-Rodríguez et al. 2007, 2016, Pérez-Noyola et al. 2021), but not in *Crataegus mexicana* DC (Rosaceae), and *Pittocaulon praecox* (Cav.) H. Rob. & Brettell (Asteraceae) (Aguilar-Rodríguez et al. 2016). In the epiphyte removal treatment, we found an increase in the number of new shoots on the branches; however, if these had damaged tissue, this would not have changed in the treatment of removal of the epiphytes. Additionally, we did not

find an effect of *T. recurvata* on the relative growth rate of the shoots or in the production of inflorescences and fruits. This suggests that the mechanism of damage could be different from hypertrophy. *Tillandsia recurvata* produces phytotoxins (de Queiroga et al. 2004, Valencia-Díaz et. al. 2012) that reduce seed germination in sympatric species of the genus *Tillandsia* (Valencia-Díaz et al. 2012). These phytotoxins can even impair tree growth when they enter the soil (Flores-Palacios et al. 2014), and therefore, these phytochemicals may act on the branches of *B. copallifera*. However, this needs to be investigated by applying *T. recurvata* extracts on the *B. copallifera* branches.

Previous studies have attempted to determine the effects of epiphytes on their phorophytes using a single response trait (e.g., Montaña et al. 1997, Soria et al. 2014, Flores-Palacios 2016). By analysing the transitions between traits, the impact of *T. recurvata* on *B. copallifera* was found to be manifested in the dynamics that impact fruit production. The combined events suggest that if the fate of a similar number of shoots is compared among treatments, branches with epiphytes will present the lowest relative fitness, while branches in which there are no epiphytes will present the highest fitness. Moreover, as expected, branches from which the epiphytes are removed will increase their fitness, but branches onto which the epiphytes are transplanted did not decrease their relative fitness. This suggests that the presence of *T. recurvata* does indeed negatively affect the phorophyte.

In the tropical dry forest studied, *T. recurvata* is not found on all the branches of its phorophytes; however, *B. copallifera* is one of the three phorophytes on which 80% of the tussocks of this epiphyte are concentrated (Vergara-Torres et al. 2010). Because the generational times are different, natural selection acts at a different speed between epiphytes and their phorophytes. If epiphytes damage their phorophytes, this would generate a selection pressure for the phorophytes only if they are massively

invaded (Flores-Palacios 2016); however, this also would generate a selective pressure on the epiphytes themselves, unless the useful lifespan of the substrate exceeds the speed of growth and reproduction of the epiphyte. It has been suggested that *Tillandsia recurvata* is a species of slow growth, with a higher risk of mortality in its seed and seedling phases, which limits its establishment and population viability on the phorophytes (Valverde & Bernal 2010). If the negative effects of the epiphyte were to perpetuate, *T. recurvata* would disappear by reducing the useful life of its own phorophytes, considering its own naturally slow growth.

Interactions can evolve until they reach an evolutionarily stable strategy (Futuyma 2013). In the studied forest, only 13.8% of the branches of *Bursera copallifera* individuals of diameter ≤ 2 cm have epiphytes (Ruiz-Cordova et al. 2014), and therefore, by not invading all the branches, *B. copallifera* is under no selective pressure to develop strategies for avoiding *T. recurvata,* as has been suggested for *Parkinsonia praecox* (Flores-Palacios 2016).

Since *T. recurvata* is autogamous (Orozco-Ibarrola et al. 2015) and a *T. recurvata* plant that colonizes a branch of *B. copallifera* has a high probability of recolonizing the same branch (Victoriano-Romero et al. 2017), if branches of *B. copallifera* die due to heavy loads of *T. recurvata*, then a density-dependent effect of *T. recurvata* could help to self-eliminate dense subpopulations. Reducing the useful life of branches of a preferred phorophyte (Cortes-Anzures et al. 2017) can have immediate ecological consequences. It could explain why only 13.8% of *B. copallifera* branches support *T. recurvata*. It is necessary to test this experimentally over a more extended period to fully understand if natural selection would act in favour of or against phenotypes of *T. recurvata* that affect *B. copallifera*.

Vascular epiphytes are an important guild of plants that increase the diversity of terrestrial ecosystems directly through their species richness and indirectly creating habitat for other organisms and through the terrestrial plants that evolved from epiphytic ancestors (Benzing 1990, Calvente *et al.* 2011, Testo and Sundue 2014). We found that *T. recurvata* can damage one of its phorophytes; this does not imply that all epiphytes damage all their phorophytes. *Tillandsia recurvata* is one of the most widespread species in the world, and several experimental studies show contradictory evidence on the effect of *T. recurvata* on their phorophytes (Flores-Palacios et al. 2014, Soria et al. 2014, Flores-Palacios 2016). The contradictory results may come from the observation of single vs. several response traits or because the effect of this epiphyte depends on the species of the phorophyte. It is necessary to continue experimenting to understand in which conditions epiphytes can be harmful to their phorophytes and how natural selection will counterbalance the adverse effects and benefits of the epiphytes in their phorophytes.

Authors' contribution. CAVT, JGGF, and AFP conceived and designed the experiments. CAVT, SVD, and AFP performed the experiments and analysed the data. CAVT, SVD, JGGF, and AFP wrote the manuscript.

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