

The recent expansion of the invasive hemiparasitic plant *Cassytha filiformis* and the reciprocal effect with its main hosts

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Research Article

Keywords: alien parasitic plants, coastal dunes, host-plant identity effects, México, parasitic plants effects, sexual reproductive success

Posted Date: January 25th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-2471502/v1>

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Version of Record: A version of this preprint was published at Biological Invasions on October 31st, 2023. See the published version at <https://doi.org/10.1007/s10530-023-03192-3>.

Abstract

Cassytha filiformis is a hemiparasitic plant that causes severe effects in its host plants. Since this decade, this alien species has been increasing its distribution towards the coastal areas of the Peninsula of Yucatán, parasitizing shrub species that play a crucial role in the containment of soil erosion. Here we studied the current distribution of *C. filiformis* along the coastal dune in northern Yucatán, recording the frequency of parasitism and the identity of its host plants. In addition, we evaluated the effect of *C. filiformis* on the sexual reproductive success of the main host plants and the effect of host species identity on *C. filiformis*'s reproductive success. We found that the distribution of *C. filiformis* occurs throughout the coastal dunes of Yucatan (covering $\approx 250\text{km}$), parasitizing 15 species. However, ca. 70% of *C. filiformis* plants occur on three common shrub species: *Suriana maritima*, *Scaevola plumieri*, and *Tournefortia gnaphalodes*. The frequency of parasitized plants by *C. filiformis* was not dependent on host plant abundance. *T. gnaphalodes* suffer a higher proportion of parasitism. The reproductive success of the three host plants was lower in the presence of the parasitic plant. On the other hand, *C. filiformis* showed higher reproductive success when parasitizing *S. maritima*. Our results suggest that *C. filiformis* has extensively invaded the Yucatán coastal dunes, significantly reducing the sexual reproduction of its host-plant species. Overall, our results suggest that *C. filiformis* has the potential to cause significant damage in the Yucatán coastal dune community.

Introduction

Globally, species invasion is one of the leading causes of biodiversity loss and ecosystem degradation (Simberloff et al. 2013; van Kleunen et al. 2018). Nevertheless, there is controversy regarding the relative importance of plant species invasion compared with other detrimental causes (e.g., habitat fragmentation and land use change). However, the consensus is extensive regarding its adverse effects on the functionality of terrestrial ecosystems and the high economic cost of losing the ecosystem services they provide (e.g., Pimentel et al. 2005; Cai et al. 2020). Alien plants (i.e., non-native or exotic plants, *sensu* Richardson et al. 2011) are among the most studied taxonomic groups, which has allowed describing general patterns of their ecology and biological characteristics (van Kleunen et al. 2010; 2018). For instance, much research has focused on assessing their competitive ability concerning native species, showing that aliens surpass natives due to their greater ability to acquire resources and higher physiological performance, which help to explain the subsequent invasion success (van Kleunen et al. 2018).

Alien parasitic species, however, have been barely studied in comparison with other parasitic plants (e.g., Kelly 1992; Pennings and Callaway 1996; Aukema 2003; Li and Song 2012; Furuhashi et al. 2016), even though the former provoke direct damages on native hosts plants and have significant effects on invaded ecosystems (Cai et al. 2020; Massanga et al. 2021). Furthermore, parasitic species are typically considered generalists (e.g., Kelly et al. 1988; Gibson and Watkinson 1992; Press 1998; Pennings and Callaway 2002), making this an apparent advantage for alien species. However, parasitic species, including aliens, show host preferences by establishing on a subset of those plants available (e.g.,

Musselman and Press 1995; Kokubugata and Yokota 2012). Thus, given the dependence of parasitic plants on nutrients and water provided by host plants, finding suitable hosts could be a crucial barrier that alien parasitic plants may face upon arrival into new ecosystems. Indeed, host identity may be a decisive factor in determining the success of the invasive species.

Which host plants are more suitable for parasitic species in a community depends on multiple factors, such as host availability and host physiological status (revised by Press and Phoenix 2005). However, a key indicator of suitable selection would be the reproductive performance of the parasites when they grow on different hosts (Heide-Jørgensen 2008; Teixeira-Costa et al. 2021). In turn, the magnitude of the effect on the reproduction and survival of preferred host plants is important because this can compromise the viability of their populations (Heide-Jørgensen 2008). Furthermore, host selection is relevant not only because of the reciprocal host-parasitic effects but also because community-level effects of parasitic plants may depend mainly on the identity and the role of parasitized species in the invaded communities (Press and Phoenix 2005). For instance, there is evidence that plant diversity increases when parasitic species grow predominantly on dominant hosts (Callaway and Pennings 1998). In contrast, when parasitic species prefer competitively subordinate hosts, the most abundant species become even more dominant, reducing thus biodiversity (Gibson and Watkinson 1992). This evidence highlights the relevance of assessing whether alien parasitic plants show host preference or not to understand better and predict their potential impact on the invaded ecosystems.

Cassytha filiformis (Lauraceae) is a hemiparasitic vine with a pantropical distribution. It mainly grows along the coastal zones (Zhang et al. 2022). In Mexico, records of this species are scarce and its occurrence has been reported mainly in the northern coast of the Yucatan Peninsula during the last 60 years (GBIF 2022). However, recent evidence suggests that during the last decade, its abundance has increased, and it is therefore considered an alien and potentially invasive species in this region (Parra-Tabla et al. 2018). This species has been characterized as a generalist parasite since it has a broad range of host plants (e.g., Li et al. 1992; Debabrata 2018). Nevertheless, Nelson (2008) reported a preference as a host for some shrubs species. Additional documented effects of *Cassytha* on host plants include decreased growth, reproduction, and death (Prider et al. 2009; Zhang et al. 2022). Furthermore, many studies show a reduction in fruit production of crops (e.g., Bakari et al. 2007; Buriyo et al. 2015; Kidunda et al. 2017; Debrabata 2018). Studies on the impact of this hemiparasite on natural ecosystems are scarcer than on crops (Zhang et al. 2022), but the evidence suggests significant effects on coastal and Island ecosystems (Nelson 2008; Cai et al., 2020). For instance, in Hawaii, Nelson (2008) observed that *C. filiformis* reduced the survival of wild and cultivated species (Nelson 2008) and in the Paracel Islands in the northern South China Sea, the invasion of this species changed the structure of the invaded communities and triggered changes in soil properties (Cai et al. 2020).

In the northern coast of the Peninsula of Yucatan, previous studies suggest that *C. filiformis* may have a relevant impact on the vegetation of coastal dunes because it parasitizes shrub species essential for the containment of soil erosion (Parra-Tabla et al. 2018; Ovando-Hidalgo et al. 2020). However, although there has been an apparent increment in the abundance of *C. filiformis* in recent years (Parra-Tabla et al.

2018) there are no studies evaluating the extent to which the distribution of the hemiparasite has expanded. Furthermore, assessments on the range of host plants and the reciprocal effect between *C. filiformis* and its main hosts are still necessary. Thus, the aims of this study were: (a) To describe the current distribution of *C. filiformis* along the northern coast of Yucatan; (b) to describe the host richness and the frequency of parasitism and to explore if *C. filiformis* shows some preference between its main hosts; (c) to test the effect of *C. filiformis* on the sexual reproductive success of its main hosts, and determine if the effect of *C. filiformis* is the same on these host species or if this effect is species-dependent, and finally (d) to test the reproductive success of *C. filiformis* on its main hosts and assess if the sexual reproductive success of *C. filiformis* is dependent on the identity of the host plant.

Materials And Methods

Study site

We studied the distribution and the parasitism of *Cassytha filiformis* on the coastal dunes plant communities along the northern coast of the Peninsula of Yucatan. Coastal dunes have a continuous distribution along the entire coast, which extends over approximately 320 km with few interruptions because of the occurrence of mangroves and coastal lagoons (Miranda 1959). The climate is hot and dry, with seasonal rainfall and a total annual reaching 760 mm. The mean annual temperature is 26°C with minimal variations along the coast (Angulo et al. 2018). The sandy coasts of the Peninsula of Yucatan contain narrow beaches, low coastal dunes, and halophyte and xerophytic vegetation (Espejel 1987; Castillo and Moreno-Casasola 1996; Angulo et al. 2018) which, besides the low rainfall and high temperatures, are exposed to other adverse abiotic conditions (e.g., tropical storms, continuous salt spray, and low nutrient availability). The dune plant community is composed of annuals (*Cakile edentula* - Brassicaceae) and perennial herbs (*Sesuvium portulacastrum* - Aizoaceae, *Lycium carolinianum* - Solanaceae, *Ipomoea pes-caprae* - Convolvulaceae), and shrubs such as *Scaevola plumieri* (Goodeniaceae) and *Suriana maritima* (Surianaceae) (Espejel 1987; Angulo et al. 2018). In this ecosystem, shrubs play an essential role as dune builders and in helping contain soil erosion, which is very relevant for these communities dominated by substrate mobility (Miller et al. 2010, Duarte et al. 2013). Therefore, shrubs are considered keystone species (Ovando-Hidalgo et al. 2020).

Study species

Cassytha filliformis (Lauraceae) is originally from Asia and has a pantropical distribution encompassing the Americas, Indomalaya, Australasia, Polynesia, and tropical Africa (Zhang et al. 2022). However, it is considered a potentially invasive alien species on the northern coast of the Peninsula of Yucatán (Parra-Tabla et al. 2018). *C. filliformis* is a hemiparasitic species of the host stems where it usually absorbs xylem-derived nutrients and water (Li and Yao 1992). Moreover, when the haustorium reaches the phloem, it can acquire photosynthetic nutrients (Balasubramanian et al., 2014). Like other species within the genus, the effects of this species on host plants include reduced growth, biomass, reproduction, and, under severe infestation, host death (Nelson 2008; Prider et al. 2009). In contrast, there is much less

evidence about the sexual reproductive success of *C. filiformis* growing on different hosts (Zhang et al. 2022). *C. filiformis* parasitizes shrubs and trees and attacks a wide range of hosts (e.g., Li et al. 1992; Nelson 2008; Buriyo et al. 2015; Debabrata 2018; Zhang et al. 2022). In coastal areas, *C. filiformis* prefers species of the genera *Scaevola* and *Tournefortia* (Nelson 2008).

Spatial distribution and plants species-hosts of the hemiparasitic alien plant *Cassytha filiformis*

The occurrence of *C. filiformis* was recorded along a 250 km transect (\times 5m wide) parallel to the coast. The sampled area covered the entire northern coast of the Peninsula of Yucatán and included the entire coastal dunes ecosystem. All individuals of *C. filiformis* and the host plant identity on which they were found were recorded along transect. Each infected host plant was examined for the presence of developed haustoria. Because of its crawling growth form, it was necessary to verify the total extent of each individual of *C. filiformis* to ensure that the number of parasites and hosts was not overestimated. Initially, at each sampling point where an individual of *C. filiformis* was found, the identity and abundance of all potential host plant species were recorded around an area of 5×5 m. However, since nearly 70% of the host plants belonged to three shrub species (see results), this record was restricted to these species. The plant cover of *C. filiformis* was measured as the area covered by the parasite on the host plants, following Mueller-Dombois and Ellenberg (1974).

Reciprocal host-plant-hemiparasitic effects on sexual reproductive success

We randomly selected 40 individuals of each host species (20 with the parasitic plant and 40 without it) to test the effect of *C. filiformis* on sexual reproductive success. These individuals were distributed along 20 km on the central area of the coast between the sites Telchac (UTM – 89.2966 21.3406) and Chabihau (UTM – 89.0597 21.3675). We measured the size (basal diameter) and plant cover (Mueller-Dombois and Ellenberg 1974) of parasitized and non-parasitized individuals. Every two weeks during the flowering and fruiting peak production of these species (September-November of 2018) (Parra-Tabla et al. 2019), the number of flowers and fruits produced by each plant was recorded. To test the effect of plant-host identity on the sexual reproductive success of *C. filiformis* every two weeks, we recorded the number of flowers and fruits produced along the flowering and fruiting production (March to April 2019) of the individuals growing on the 20 randomly selected parasitized shrubs.

Statistical analyses

We performed a Chi-test (2×3) (with and without parasitic plants \times three host species) to test the independence of the frequency of plants with and without the parasite among the main plant hosts of *C. filiformis* (Greenwood and Nikulin 1996). Specifically, we were interested in determining if there were statistically significant differences between the observed and expected frequencies of parasitism status (with and without the parasite) across the main plant hosts. In addition, to test if *C. filiformis* attacks larger individuals (size and host plant cover), t-tests for each host species were performed to compare plants with and without the parasites. The Chi-test and the t-test were performed with the procedure *freq* and *t-test* in SAS (2002). The magnitude of the effect of *C. filiformis* on the sexual reproductive success

of the main host-plant species was tested by calculating the Hedges' effect size (Hedges and Olkin (1985), as Hedges' $g = (W_o - W_s) / SD$ pooled. Where W_s are the mean values of the total production of flowers, fruits, and fruit-set (total number of mature fruits /total number of flowers), of no parasitized plants, and W_o for parasitized plants. SD is the pooled weighted standard deviation (Hedges and Olkin 1985).

Finally, to evaluate the effect of plant-host identity on the sexual reproductive success of *C. filiformis*, a generalized mixed linear model (GLMM) was performed using host identity as a fixed effect and each individual host plant as a random effect. We included host-plant and *C. filiformis* plant coverages in this model as covariates. *Post-hoc* significant differences between host species were tested with multiple paired tests. We used log-normal error distribution with an identity link function for the number of flowers, fruits, and fruit sets (Littell et al. 2006). For the three variables analyzed, this type of error and linkage function showed the best fit (Akaike information criterion). These analyses were carried out using the GLIMMIX and the *pdiff* procedures (for the multiple paired tests) in SAS (2002).

Results

Spatial distribution and plants species-hosts of the hemiparasitic alien plant *Cassytha filiformis*

The current distribution of *C. filiformis* encompassed practically the entire sand dunes of the northern coast of the Yucatán peninsula (Fig. 1). We recorded 943 individual plants of *C. filiformis* growing on 15 plant species. Eight were trees and shrubs, and seven were herbs (TS1). However, ca. 70% (N = 659) of the parasitized plants corresponded to three shrub species, namely *Scaevola plumieri* (Goodeniaceae), *Tournefortia gnaphalodes* (Boraginaceae), and *Suriana maritima* (Surinaceae). *T. gnaphalodes* showed the highest percentage of plants with the parasite (76.7%) vs. without (23.3%) (N = 255). *S. maritima* followed in the intensity of parasitism (66.7% with vs. 33.3% without, N = 270), and, finally, *S. plumieri* (69.2% with vs. 30.8% without the parasite) (N = 338). We found that the frequency of parasitism status was not dependent on the abundance of the host plant species ($\chi_2^2 = 7.15$, $P = 0.028$). We observed that, in *S. maritima* and *S. plumieri*, the number of plants with the parasite was lower than expected. In turn, *T. gnaphalodes* (Fig. 2) had more parasites than expected by chance. Consequently, the number of plants without the parasite was lower than expected for *S. plumieri* and *S. plumieri* but higher in *T. gnaphalodes* (Fig. 2).

Size and plant cover between parasitized and not parasitized plants did not differ in *S. maritima* and *S. plumieri* ($t \leq 1.7$, $P > 0.05$, in all cases). In contrast, the results for *T. gnaphalodes* revealed that taller plants with higher plant cover were significantly more parasitized ($t_{(38)} = 2.6$, $P = 0.01$, and $t_{(38)} = 2.12$, $P = 0.04$, respectively).

Reciprocal host-plant-hemiparasitic effects on sexual reproductive success

The flower and fruit production of hosts without the parasite was almost twice that of plants with the parasite (Fig. 3). *C. filiformis* significantly decreased the number of flowers and fruits produced by the

three host-plant species (Fig. 3; *Hedge's* effects size ≥ -1.32 , in all cases, $P \leq 0.01$). In addition, *C. filiformis* significantly affects the fruit-set of *S. maritima* and *T. gnaphalodes* (Fig. 4a, c; *Hedge's* effects size ≥ -2.18 , $P \leq 0.01$) but did not affect the fruit-set of *S. plumieri* (Fig. 4b; *Hedge's* effect size = -0.27 , $P = 0.2$).

Hosts' identity also significantly affected the total number of flowers and fruits produced by *C. filiformis* (Table 1). Overall, *C. filiformis* produced more flowers and fruits and showed a higher fruit set when it grew on *S. maritima* (Fig. 5). Paired tests showed that *C. filiformis* produced significantly more flowers when growing on *S. maritima* than on *S. plumieri* ($t_{(45)} = 4.75$, $P < 0.001$) but did not differ regarding *T. gnaphalodes* ($t_{(45)} = 1.16$, $P = 0.25$). The number of flowers produced by *C. filiformis* was significantly higher when growing on *T. gnaphalodes* than on *S. plumieri* ($t_{(45)} = 4.45$, $P < 0.001$) (Fig. 5a).

Table 1

Effect of the identity of the host species, host cover, and parasitic cover on the flower and fruit production and fruit set (total fruits/total flowers) of the alien hemiparasitic *Cassytha filiformis*

Effect	Response variable		
	Flower production	Fruit production	Fruit set
Species host identity	$F_{(2, 45)} = 14.8$, $P < 0.001$	$F_{(2, 45)} = 44.72$, $P < 0.001$	$F_{(2, 45)} = 29.9$, $P < 0.001$
Host plant cover	$F_{(1, 45)} = 0.12$, $P = 0.72$	$F_{(1, 45)} = 0.17$, $P = 0.72$	$F_{(1, 45)} = 1.23$, $P = 0.27$
<i>Cassytha filiformis</i> cover	$F_{(1, 45)} = 1.62$, $P = 0.2$	$F_{(1, 45)} = 0.01$, $P = 0.2$	$F_{(1, 45)} = 0.89$, $P = 0.34$

The number of fruits produced by *C. filiformis* was significantly higher on *S. maritima* compared to *S. plumieri* and *T. gnaphalodes* ($t \geq 4.3$, $P < 0.01$, in both cases; Fig. 5a). There were no significant differences between fruit production of the parasite when growing on both species ($t_{(45)} = 0.2$, $P > 0.1$; Fig. 5a). Finally, the fruit set of *C. filiformis* was significantly lower on *T. gnaphalodes* compared with *S. maritima* and *S. plumieri* ($t \geq 6.13$, $P < 0.001$, in both cases; Fig. 5b), and we did not observe significant differences between these species ($t_{(45)} = 1.56$, $P = 0.12$; Fig. 5b). Neither plant-host cover nor *C. filiformis*' plant cover affected significantly the number of flower and fruits produced or fruit-set (Table 1).

Discussion

Our results show that the alien hemiparasitic parasitic plant *Cassytha filiformis* is widely distributed throughout the northern coast of Yucatán, occupying a large proportion of the entire coastal dune. According to historical records, this species has rarely been reported in the last 60 years (GBIF 2002). Similarly, in systematic surveys of coastal vegetation over the last 30 years and early 2000s, *C. filiformis* had not been reported in these ecosystems (Espejel 1987; Flores and Espejel 1994; Castillo and Moreno-Casasola 1996; Torres et al. 2010). However, in a recent study encompassing the analysis of nine communities distributed along the coastal dune of Yucatán, Parra-Tabla et al. (2018) observed that this

species was frequent and, in some communities, was among the most abundant species. Those surveys and the present work results suggest that *C. filiformis* has been successfully invading the northern coast of Yucatan over the last decade.

Our results also showed that *C. filiformis* can occupy many host plants (15 species). However, of the observed 15 host species of *C. filiformis*, six were herbaceous (Table Supplementary 1), and *C. filiformis* did not develop haustoria on these species. Previous studies found that, when searching for suitable hosts, parasitic plants show nastic movements by rolling up the stem of potential hosts but develop haustoria only on those that appear suitable (Kelly 1990, 1992). This colonization strategy seems to be the case for species such as *Agave angustifolia*, *Bidens pilosa*, and *Porophyllum punctatum*, where we observed that after *C. filiformis* coiled on them, it 'rejected' the potential hosts without developing haustoria and continued its exploration (Fig. 6). This pattern contrasts with that observed for *S. plumieri*, in which the penetration of haustoria was evident (Fig. 6). This means that in the coastal dunes of Yucatán, the number of 'true hosts' of *C. filiformis* is reduced. Previous reports in coastal and forest ecosystems showed that *C. filiformis* parasitizes many tree and shrub species (Nelson 2008; Kokubugata and Yokota 2012; Buriyo et al. 2015; Debrabata 2018; Cai et al. 2020). However, although in the Yucatán coastal dunes we observed that *C. filiformis* grew on eight tree and shrub species, three of the shrubs accounted for almost 70% of parasitism, suggesting a remarkable host preference for these shrubs. Tree species such as *Metopium brownie*, *Conocarpus erectus*, and other common shrub species in coastal dunes such as *Maytenus phyllanthoides* and *Coccoloba uvifera* (Espejel 1988; Torres et al. 2010; Angulo et al. 2018) showed minor or no parasitism. In coastal ecosystems, Nelson (2008) suggested that *C. filiformis* prefers species of the genera *Tournefortia* and *Scaevola* (Nelson 2008).

The above mentioned observations are consistent with our results since the percentage of *T. gnaphalodes*, and *S. plumieri* with the parasite was high (76.7% and 70.72%, respectively). However, we also observed a high percentage of *S. maritima* with the parasite (66.7%). Furthermore, we observed significant differences between observed and expected frequencies of plants with and without the parasite. Specifically, we observed that *T. gnaphalodes* showed more individuals with the parasite than expected, while *S. maritima* and *S. plumieri* showed the opposite pattern. These results suggest that despite the high parasitism observed in the three shrub species, *C. filiformis* predominantly grows on *T. gnaphalodes*. Moreover, only in the case of *T. gnaphalodes* plants with a larger basal diameter and plant cover were more attacked. The above means that *T. gnaphalodes* is not only a preferred host, but also those larger individuals are more parasitized. Selection effects according to host size were observed in *Cassytha pubescens*, where the use of smaller hosts resulted in lower biomass of this parasitic plant (Cirocco et al. 2020).

The mechanisms by which parasitic plants select the 'best' host are complex (Press and Phoenix 2005, and see Kaiser et al. 2015; Li et al. 2015). However, the selection of host plants is related to factors such as the certainty of having resources for extended periods or access to limited resources such as water availability and nutrients (Kelly et al. 1988; Gibson and Watkinson 1992; Li et al. 2015; Girocco et al. 2020). The above explains the preference of parasitic species for shrub and tree life forms (Press and

Phoenix 2005), particularly in coastal dune ecosystems where the availability of water and nutrients are limiting factors (Martínez and Psuty 2004). In this case, it is expected a preference for long-lived hosts. In addition, host selection by *Cassytha* seems to be related to the morphological characteristics of the host plant since better performance occurs when growing on shorter trees and shrubs (Zhang et al. 2022). Specifically, *C. filiformis* prefers low and branched woody host plants (Werth et al. 1979). This preference would explain why it occupies a low proportion of trees such as *Metopium brownei* or *Conocarpus erectus*, which are taller, erect, and have less racemose growth than *T. gnaphalodes*, *S. plumieri*, and *S. maritima*.

However, the evidence that *C. filiformis* parasitized a high number of tree species in different ecosystems, including coastal communities (Li et al. 1992; Nelson 2008; Buriyo et al. 2015; Debabatra et al. 2018; Cai et al. 2020), suggests that other factors are related to host plant selection. For instance, the thickness or roughness of the branches to be penetrated by the haustorium, host metabolites concentration, or the presence of possible host plant chemical defenses, has been reported in other parasitic species, including *Cassytha* (Press and Phoenix 2005; Heide-Jørgensen 2008; Li et al. 2015; Furashi et al. 2016; Facelli et al. 2020). The study of these characteristics could help to understand the differences between the frequency of parasitized host species and the performance of parasitic plants on different host plants. For instance, despite the preference for *T. gnaphalodes*, our results showed a significant effect of host identity on the three fecundity variables of *C. filiformis*. *S. maritima* seems to be the best host because of the higher flower and fruit production of *C. filiformis* observed when growing on this host. Thus, other host plant traits should be analyzed in future studies to understand better the mechanisms of host preference of *C. filiformis* when invading the coastal dunes of Yucatán.

Importantly, our results showed a significant reduction in the fecundity of the three main hosts independently of host preference. The analyses of the effect of size showed that parasitized plants suffered about a twofold reduction in the number of flowers and fruits produced and on fruit set. Like in other hemiparasitic species, the effect of *C. filiformis* on their hosts is triggered by the absorption of nutrients, water, and photosynthetic nutrients (Press and Fox 2005; Li and Yao 1992; Balasubramanian et al., 2014; Furuhashi et al. 2016). This decrease in resources needed to support reproductive structures explains the extensive reduction in the fecundity of *C. filiformis*' hosts.

Our observations confirmed that: a) Colonization by *C. filiformis* does not occur evenly among host plants, and its impact on host fecundity varies between species. b) Diminished host fecundity may have relevant demographic impacts on the three hosts, even though they also have asexual reproduction (see Parra-Tabla et al. 2018). c) One of the most relevant outcomes of the occurrence of the parasite on the coastal dunes vegetation would be the potential reduction in the recruitment of its host plant species through sexual reproduction (see Suárez-Mariño et al. 2019; Parra-Tabla et al. 2021). Finally, although we did not measure the effect of *C. filiformis* on host survival, it is probably similar to that observed in other species, where the mortality of plants with the parasite increased (Li and Huang 1991; Nelson 2008; Pride et al. 2009). If this happens in the coastal dunes of Yucatán, as some preliminary field observations

suggest (Parra-Tabla obs. pers.), the impact of *C. filiformis* on the demography of their primary hosts and the consequences on the community could be even more severe.

Different studies have suggested that the community-level effect of parasitic plants depends mainly on the identity of the attacked plant species (Press and Phoenix 2005). In the coastal dunes of Yucatán, the relevance of the high frequency of attacks on *T. gnaphalodes*, *S. plumieri*, and *S. maritima* by *C. filiformis* relates to the sand binding-dune building features of the three hosts (Ovando-Hidalgo et al. 2020). These keystone species facilitate the establishment of multiple plant species. Thus, cascading impacts would be expected at the community level as the keystone plants are lost (Acosta et al. 2009; Miller et al. 2010; Duarte et al. 2013). Although it is still necessary to monitor the demographic impact of *C. filiformis* on its hosts, our findings suggest that the presence of the parasite can cause significant damage to the Yucatán coastal dunes communities. Given the current extensive distribution of *C. filiformis* along the northern coast of the Peninsula of Yucatán, it is imperative to launch effective control measures for this species in the short term.

Declarations

Acknowledgments

VPT thanks Instituto de Ecología A.C. (INECOL) for the support during his sabbatical stay. The authors thank Jesús Hinojosa for his help during the fieldwork and Debora Lithgow for her help in creating the figure of the *C. filiformis*' distribution.

Funding

This work was supported by the Consejo Nacional de Ciencia y Tecnología (CONACyT, Grant 248406).

Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Conflict of interest. The authors declare no conflicts of interest.

Author Contribution

VPT and JTG conceived, designed the research, and collected fieldwork data. VPT, MLM, and JGF wrote, edited, and led the writing of the manuscript. All authors gave critical contributions to drafts and final approval for publication.

Data availability

The data sets generated and analyzed during this study are available from the corresponding author upon request.

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Figures

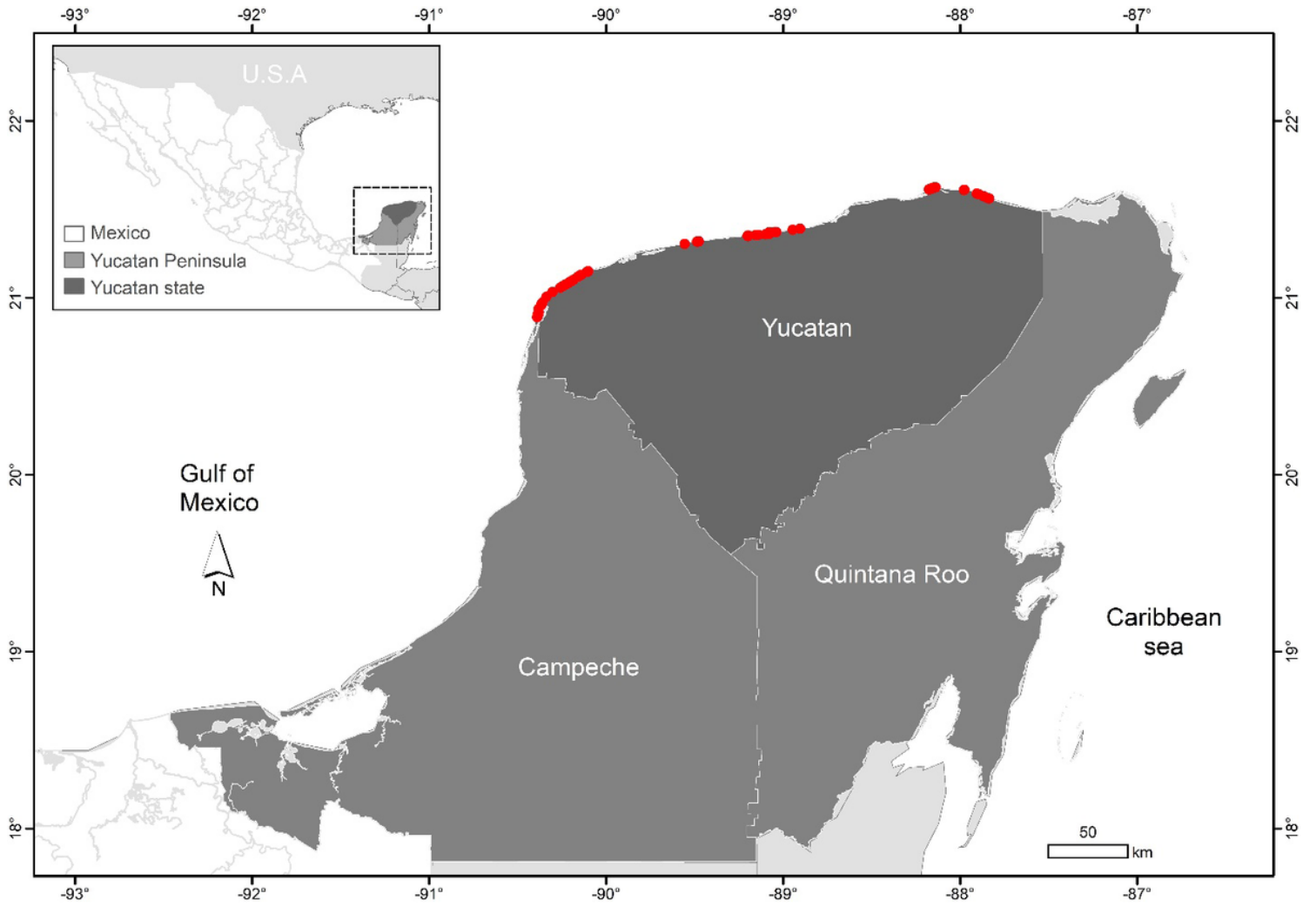


Figure 1

Distribution (red dots) of *Casytha filiformis* along the northern coast of the Peninsula of Yucatán, México

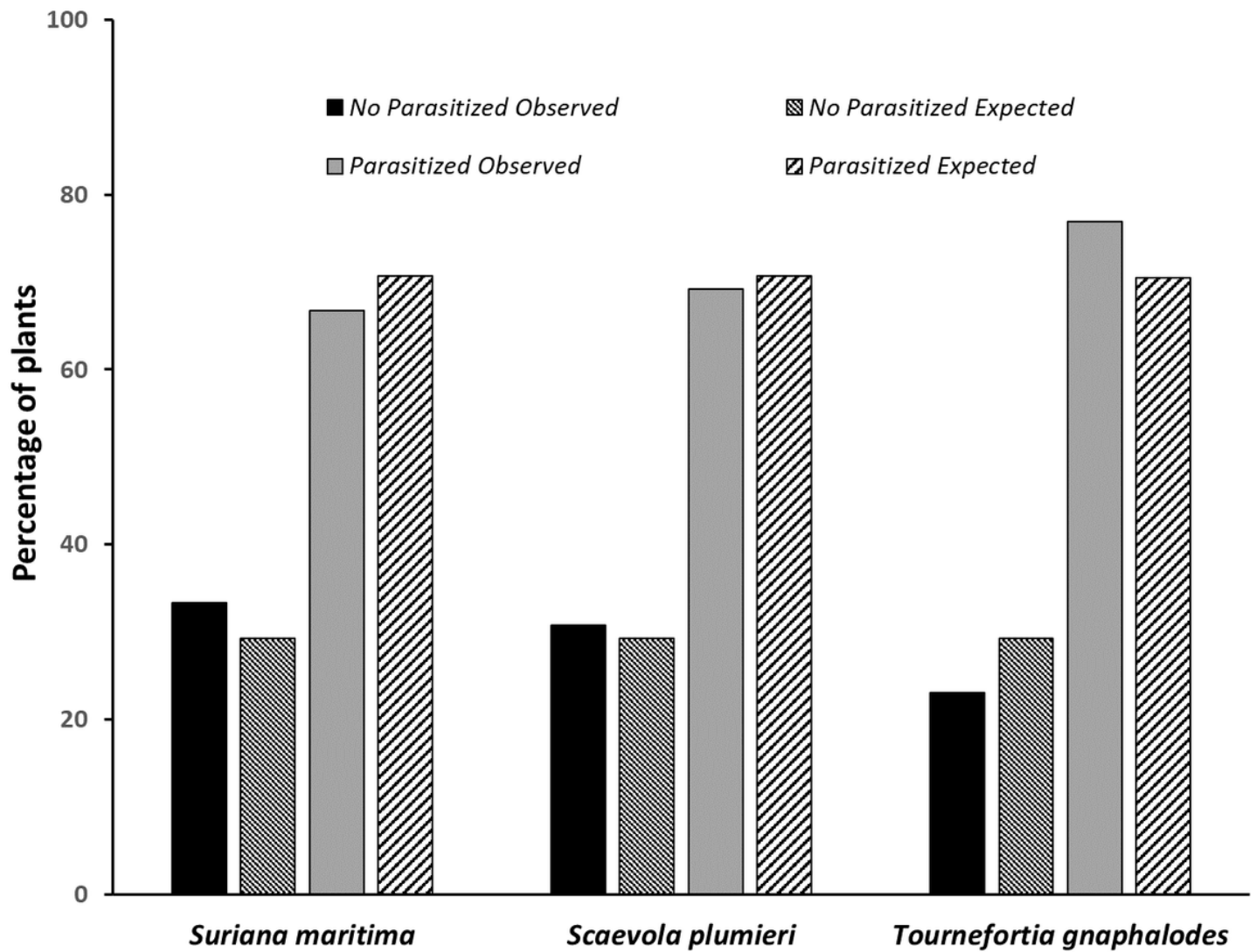


Figure 2

Percentage of observed and expected hosts with and without the parasitic plant *Cassytha filiformis* on the coastal dunes of the Peninsula of Yucatán

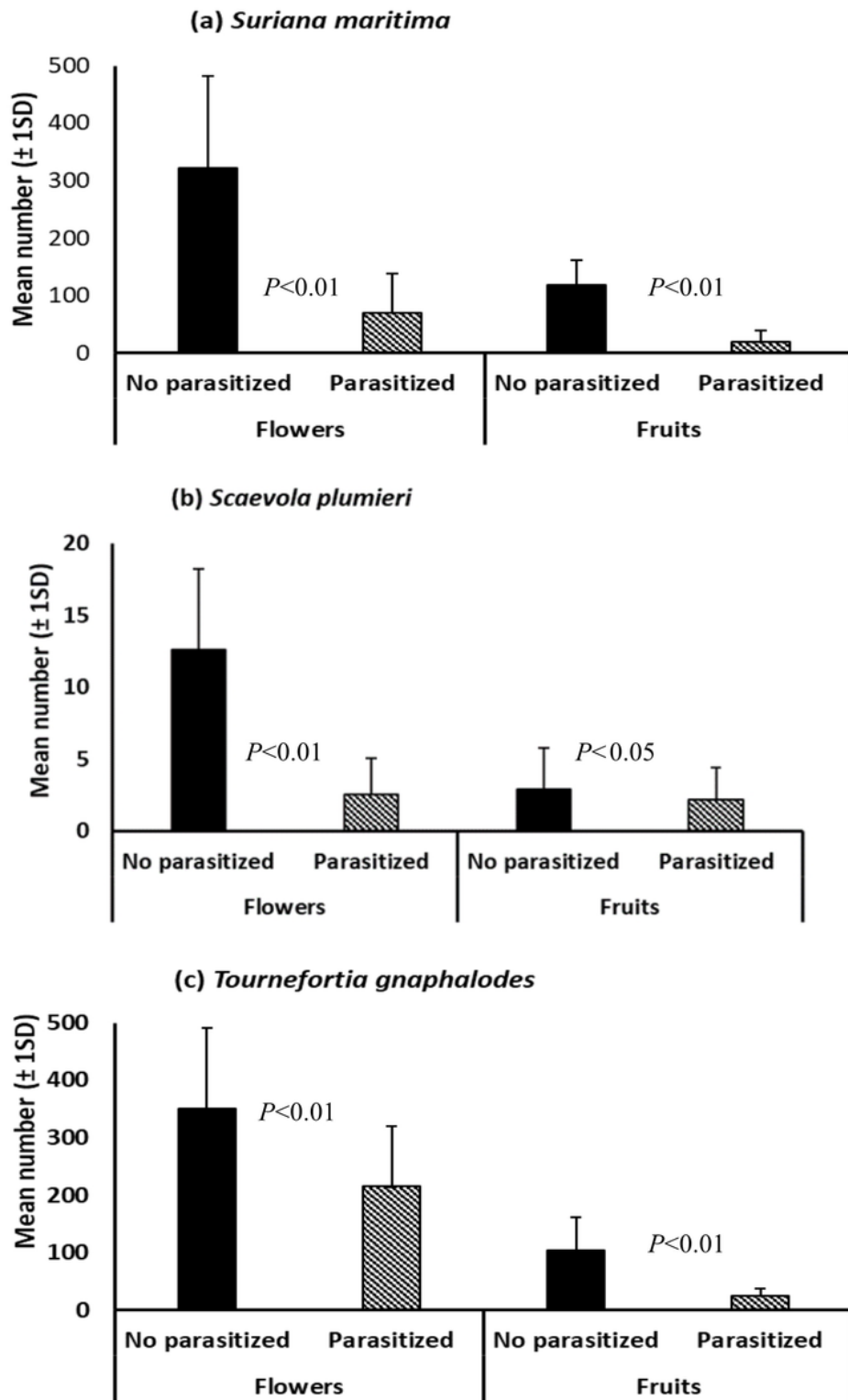


Figure 3

3 Mean number (\pm 1SD) of flowers and fruits of plants with and without the hemiparasitic *Casytha filiformis* on the coastal dunes of the Peninsula of Yucatán. Significance *P*-values for the hedge effect size analyses are shown (see Fig. S1)

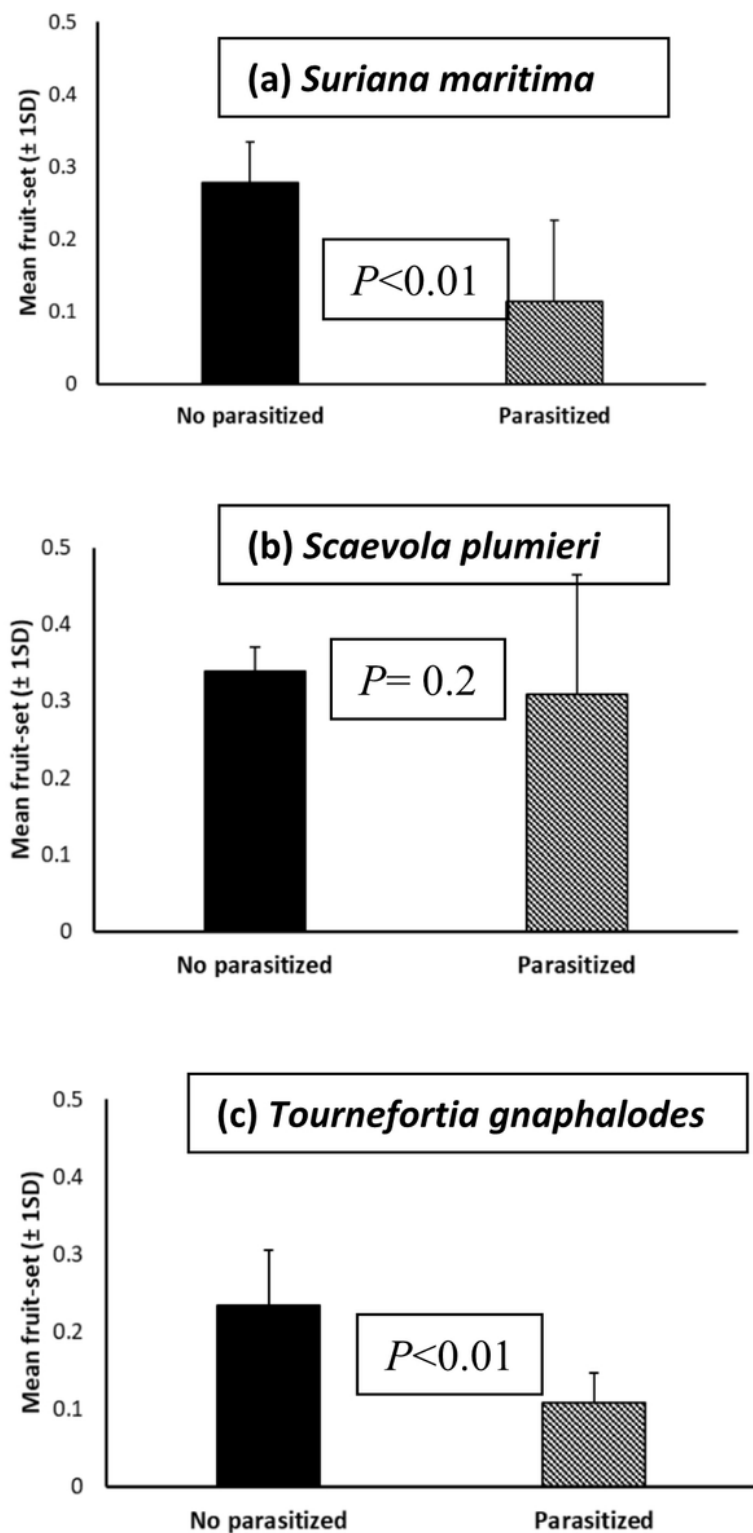


Figure 4

Mean fruit set (\pm 1SD) of plants with and without the hemiparasitic *Casytha filiformis* in the coastal dunes of the Peninsula of Yucatán. Significance P -values for the hedge effect size analyses are shown (see Fig. Supplementary 2)

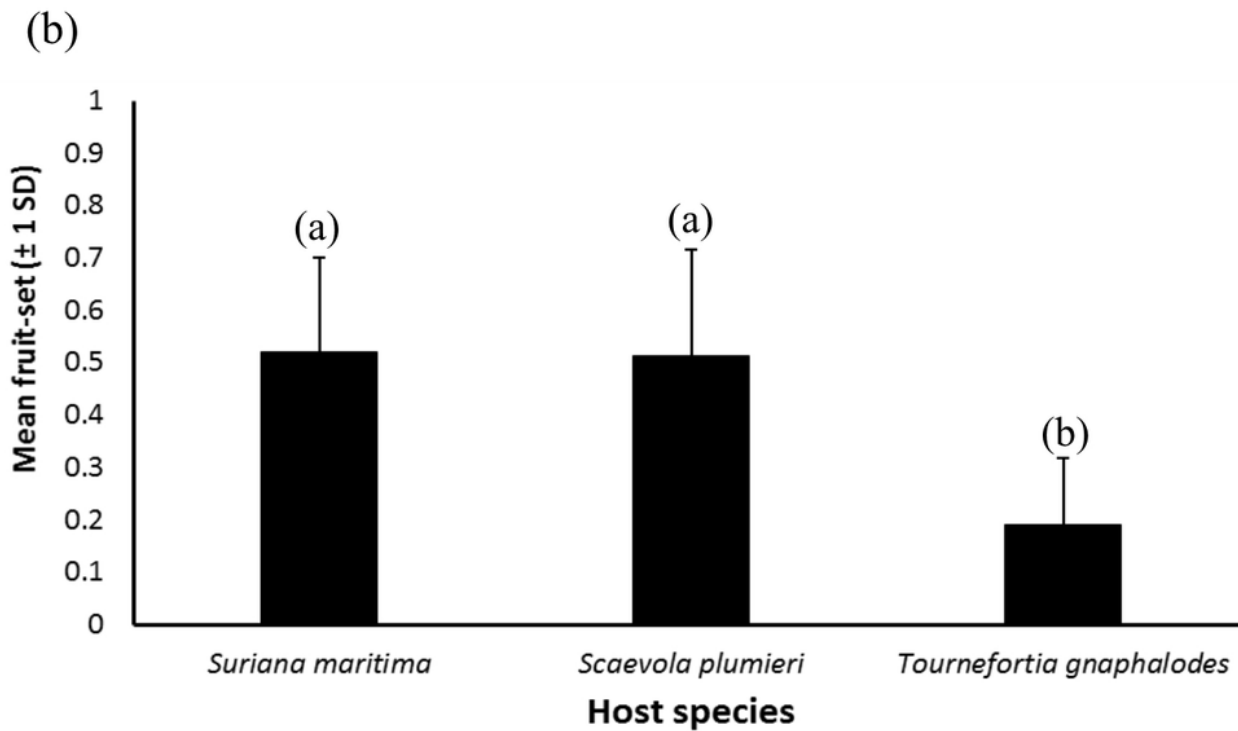
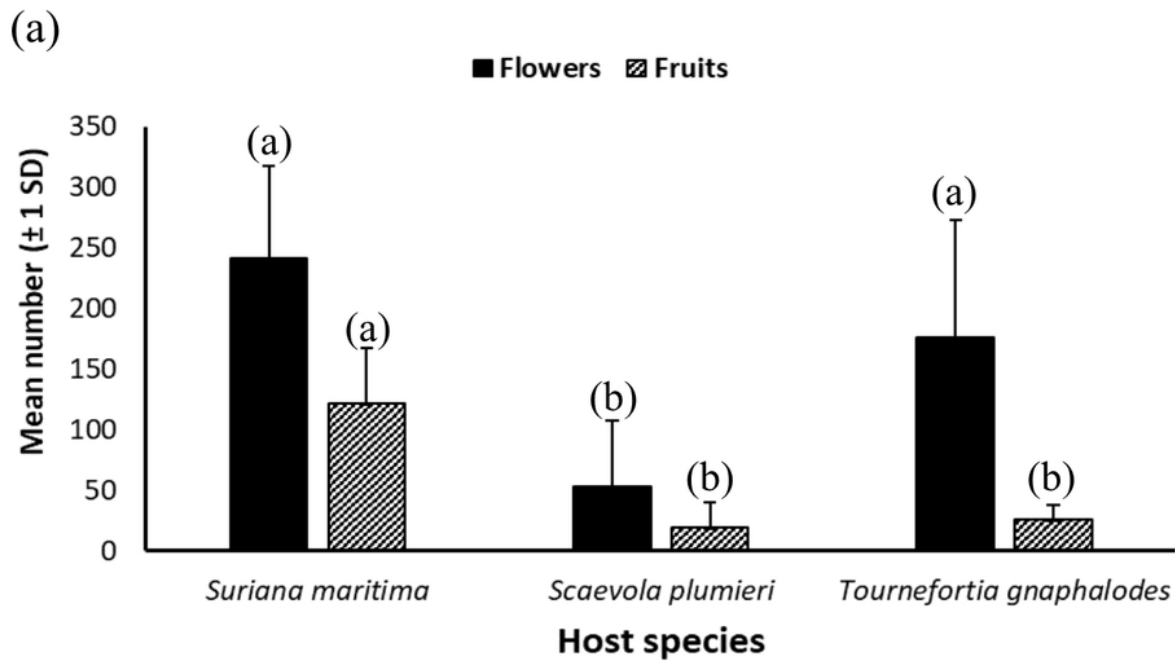


Figure 5

a) Flower and fruit production and b) fruit-set (mean ± 1 SD) of the hemiparasitic alien plant *Casytha filiformis* growing on three host-plant species in the coastal dunes of the Peninsula of Yucatán



Figure 6

Casytha filiformis attached on *Scaevola plumieri* (left) and *Porophyllum punctatum* (right) (Photo credit: Alexander Suárez Mariño)

Supplementary Files

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