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Short communication

Susceptibility to parasitism by the mistletoe *Phoradendron quadrangulare* (Kunth) Griseb on its host *Guazuma ulmifolia* Lam may increase with host size

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A R T I C L E I N F O

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A B S T R A C T

Host-parasite interactions and host susceptibility are key traits in understanding trophic energy transfer, nutrient movement and general macro-ecoevolutionary dynamics of mistletoe systems and plant-plant interactions. This research investigates host susceptibility and size-dependent interactions of the mistletoe *Phoradendron quadrangulare*, a widely distributed species, on *Guazuma ulmifolia*. We studied the interplay between mistletoe load and host tree size, while also exploring the allometric relationship between host branch size and mistletoe size. A field surveys on 67 trees revealed varying mistletoe loads, with most trees showing no occurrence of *P. quadrangulare*. Parasitized trees had significantly larger diameters at breast height (DBH) than non-parasitized trees. The susceptibility of host trees to mistletoe parasitism increased with increasing DBH, indicating a positive relationship between host size and mistletoe prevalence. Furthermore, mistletoe stem diameter was found to be influenced by the diameter of the host branch suggesting that larger host trees provide more substrate for larger-sized parasites and surface area for mistletoe colonization, potentially contributing to the parasite's survival and prevalence. This study also highlights the importance of host size in mistletoe presence and performance and provides insights into the broader eco-evolutionary dynamics and conservation strategies needed to conserve mistletoes, an often-underappreciated keystone taxa.

1. Introduction

Among parasitic taxa, it is well established that parasite transmission and dispersal is dependent on parasite exposure, host presence and susceptibility to infection. Plant parasites are no exception, which through plant-plant interactions acquire resources and transfer energy from their host needed for growth and survival, effectively making them consumers (Hull and Leonard, 1964; March and Watson, 2010; Muche et al., 2022; Nabity et al., 2021; Tesitel et al., 2010; Zhang et al., 2023). Plant parasites depend completely (holoparasites) or partially (hemiparasites) to their host thus influencing intra/interspecies interactions and coevolutionary histories (Nickrent, 2020). However, we know relatively little about how host susceptibility influences plant-parasite establishment at local scales, a fundamental aspect of the parasite's eco-evolutionary dynamics, particularly that of stem parasites, such as mistletoes.

Mistletoes, recognized as hemiparasites of trees and shrubs, belong to the families Loranthaceae, Misodendraceae, and Santalaceae (Santalales), where the evolution of stem parasitism has independently arisen multiple times from root parasitic ancestors (Liu et al., 2018; Nickrent et al., 2010; Teixeira-Costa and Davis, 2021; Vidal-Russell and Nickrent, 2008). They exhibit autonomous germination of their seeds that occurs directly on host branches, effectively tapping into the xylem of their favored host of which they acquire water, carbon, and nutrients (Teixeira-Costa and Davis, 2021). Within the family Santalaceae, the Neotropical and Neartic genus *Phoradendron* (∼240 species) is entirely

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Fig. 1. a) Specimen of *Phoradendron quadrangulare* in situ with the characteristic orange fruits (photo by Lex García). b) *P. quadrangulare* on *Guazuma ulmifolia* in the Palo Verde Biological Station, Costa Rica. The host can be seen on the top left and the mistletoe is in the center of the image (photo by Luis Santiago-Rosario).

comprised of parasitic stem plants that grow on woody angiosperms and gymnosperms and is considered the most speciose mistletoe genus of the family (Kuijt, 2003; Smith et al., 2001). The genus is recorded parasitizing the orders Cupressales, Fabales, Fagales, Lamiales, Malvales, Malpighiales, Myrtales, Pinales, Santalales, among others, with species varying in their host specificity (Calvin and Wilson, 2009; Calvin and Wilson, 1995; de Abreu et al., 2010; Kuijt, 2003; Lobo, 2016; Overton, 1997).

One of the most widely distributed species within the genus is the Guacimilla de Canario, *Phoradendron quadrangulare* (Santalaceae: Santalales), which exhibits a wide range, from northern Mexico to northern Argentina, with documented presence in the Caribbean region (Francis, 2004; Kellogg and Howard, 1986; Lobo, 2016; Moreno-Ramírez et al., 2018). This species has been reported to parasitize at least 18 orders of plants suggesting a relatively low host specificity across its range (Dettke and Waechter, 2014; Francis, 2004; Lobo, 2016). It produces bright-yellow fruits that attract birds (Fig. 1a), which consume the fruits and subsequently excrete seeds covered in viscous slime onto host branches, thereby facilitating local seed dispersal to susceptible host trees (Davidar, 1987).

In the vicinity of the Palo Verde Biological Station, Guanacaste, Costa Rica, *P. quadrangulare* exclusively parasitizes the West Indian elm, *Guazuma ulmifolia* (Malvaceae: Malvales, Fig. 1b). Within the canopy, this mistletoe species forms haustorial connections with *G. ulmifolia*, and the prevalence of the connections varies among individual host trees. This observed variation in mistletoe load and host preference by *P. quadrangulare* piqued our interest, prompting us to investigate whether the size of the host tree, as measured by the diameter of breast height (DBH), influenced host susceptibility to mistletoe parasitism. We expected that the larger the tree the higher the probability of mistletoe presence in the tree canopy. Additionally, we also sought to examine whether mistletoe size, measured as mistletoe main stem diameter, scaled with host branch sizes to better understand how local host-mistletoe interactions impact mistletoe performance.

2. Materials and methods

This study was conducted at the seasonally dry deciduous forest of Palo Verde Biological Station, Guanacaste, Costa Rica (10°23′50″N 85°19′24″W) in February 2023 during the dry season, covering an area of ~0.23 km^2. Sixty-seven trees, representing all the *G. ulmifolia* trees in the area studied, were assessed for mistletoe presence and breast height diameter (DBH), a commonly used proxy for assessing tree growth and size (Sumida et al., 2013). Because we sampled them during the dry season, mistletoes were easily identifiable given that their deciduous host lack leaves and the mistletoe preserve them during this time. Additionally, when possible, the branch where the mistletoe was located was removed with an extendable pruner, and the diameter of the main stem of the mistletoe and the immediate host branch with the haustorium was measured in centimeters with a diametric meter.

To assess whether parasitized trees differ in their DBH from non-parasitized trees, we used a *t*-test. Additionally, we performed a hurdle model to test whether host susceptibility increases as a host DBH increases by implementing the function *'hurdle'* in the package "pscl" (Zeileis et al., 2008). Briefly, the hurdle model is a two-component mixture model, with the first being the probability of attaining a value of zero and the second part modeling the probability of non-zero values (Zeileis et al., 2008). The hurdle model is often used when there is an excess of zeroes in the data. We performed the hurdle model for the dependent variable of parasite count while considering host DBH as the independent variable. We used a negative binomial distribution, given that a Poisson distribution approach resulted in overdispersion (Feng,

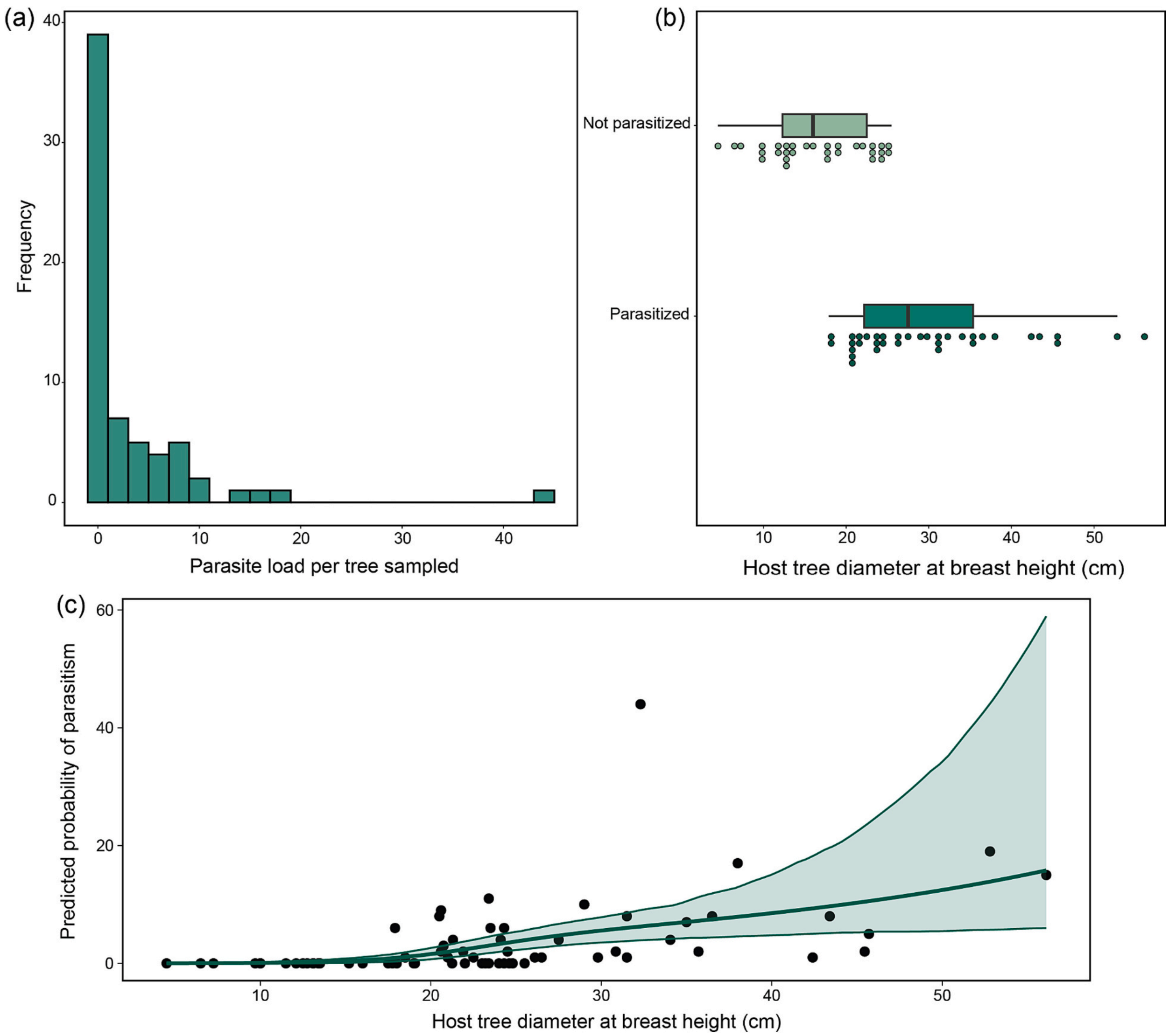

Fig. 2. a) Frequency of parasitic load across trees sampled. b) Host DBH (cm) for parasitized and not parasitized trees. c) Predicted probability of parasitism as tree DBH (cm) increases. Dots indicate observed data, and the green line depicts the predicted probability of parasite load based on the hurdle model with 95% confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2021; Taylor et al., 2022).

We performed a linear regression on log-transformed data to test for mistletoe stem diameter (cm) constraint across host branch sizes (cm). All statistical analyses were performed in R (R Core Team, 2023).

3. Results and discussion

Parasite load was found to vary among host trees, with 31 trees showing no occurrence of *P. quadrangulare*. Among the trees that hosted *P. quadrangulare*, the mean parasite load was 6.46 ± 1.36, ranging from a minimum of one to a maximum of 44 mistletoes on a single host tree (Fig. 2a). Across the trees sampled, the mean DBH of parasitized trees (30.15 ± 1.67 cm) was significantly higher (~83.54%) compared to non-parasitized trees (16.40 ± 1.09 cm; $t_{(57.4)} = 6.87$, $p > 0.0001$, Fig. 2b).

The susceptibility of host trees to mistletoe parasitism was found to increase as DBH increased. According to the hurdle model, the baseline odds of a tree having a positive parasite count vs. zero were 0.001. However, these odds increased 1.37 times with each DBH unit increase in *G. ulmifolia* DBH when parasite counts were recorded. The baseline for the trees that have been parasitized was 1.12 and increased by a host DBH unit increase by 1.04 suggesting that as the tree grew larger, the probability of having more parasites increases proportionally (Table 1). The range of DBH among trees with mistletoes varied from 17.9 cm (smallest) to 56.1 cm (largest). Trees with a DBH of <17.9 cm were not parasitized by *P. quadrangulare* (Fig. 2c).

Table 1
Hurdle model outcome for parasite load across host DBH.

Count model coefficients (truncated negative binomial with log-likelihood)					
Variables	Estimate	Standard Error	Z value	*p*-value	$e^{(Estimate)}$
Intercept	0.112	0.852	0.131	0.896	1.118
DBH	0.044	0.025	1.782	0.075	1.04
Zero-hurdle model coefficients (binomial with logit link)					
Intercept	−6.822	1.872	−3.645	0.0003	0.001
DBH	0.314	0.085	3.715	0.0002	1.369

Furthermore, our findings also indicate that *P. quadrangulare*'s size (measured as stem diameter) is limited by the diameter of the host branch of *G. ulmifolia*. Our results reveal a significant and positive linear relationship between mistletoe stem diameter (cm) and host branch

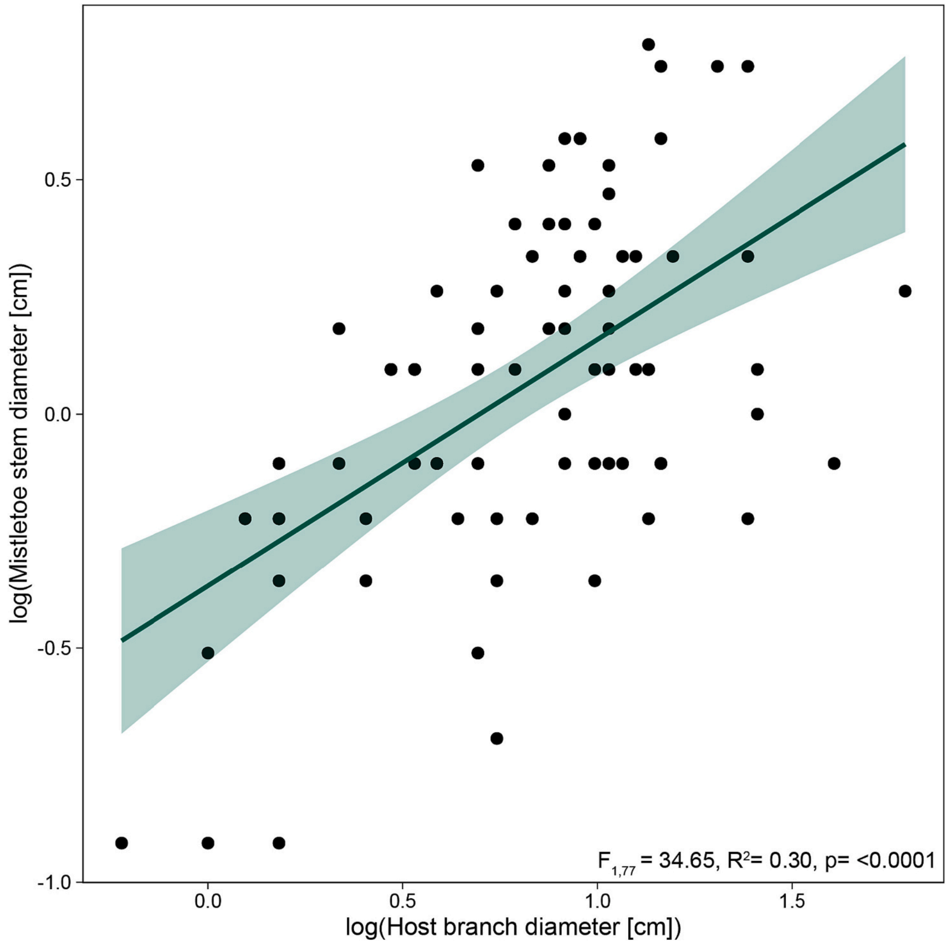

Fig. 3. Allometric relationship between host branch diameter (cm) and mistletoe stem diameter (cm).

diameter (cm) and the site of haustorium formation ($F_{1,77} = 34.65$, $R^2 = 0.30$, $p \leq 0.0001$, Fig. 3).

Hosts' susceptibility to parasitism reflects life history traits essential for mistletoe survival. Mistletoes rely on their hosts for substrate, nutrients, and water uptake, thus impacting mistletoe species' physiological, ecological, and evolutionary responses (Smith et al., 2001). According to our findings, the probability of *G. ulmifolia* susceptibility to *P. quadrangulare* parasitism and prevalence increases as trees increase in size, potentially due to the increased surface area and availability of branch-tappable xylem (Sargent, 1995). Similar findings have been observed for *Loranthus europaeus* Jacq. in Europe and *Phragmenthera dschallensis* (Engl.) M.G. Gilbert (Loranthaceae) in Africa suggesting that host size influences mistletoe's establishment and survivorship while also increasing host susceptibility as host increments in size, a pattern that may be generalizable across mistletoe taxa (Matula et al., 2015; Roxburgh and Nicolson, 2008). A confounding effect in our study might be related to the time the host has been present in the forest, i.e., the longer a tree is in the forest the more susceptible it could be and how that is hard to disentangle from size. Yet, since DBH is a proxy for tree size and size is correlated with time of growth (Sumida et al., 2013; Trouillier et al., 2019), we find our study to be relevant, yet future experiments considering dendrological studies of tree age could be used to disentangle host tree age and size and how they might be influencing parasitic load.

Here we discuss several alternative hypotheses that could also explain mistletoe-host interactions across a canopy. The tree-age hypothesis posits that larger, typically older trees may undergo heightened parasitism, potentially influenced by their prolonged presence, with tree age often correlating with DBH (Lukaszkiewicz and Kosmala, 2008; Su et al., 2021). Moreover, another potential contributing factor might be related to the host-quality hypothesis. Variation in host quality may arise due to differential access to water, light, and nutrient availability, potentially diminishing the tree's defense capacity against mistletoe infections, particularly in periods of seasonal adversity or geological variation (e.g., proximity to a water source) (Watson, 2009; Watson et al., 2007). Lastly, the potential impact of herbivores on mistletoe presence and survivorship warrants consideration. Numerous insects and ground mammals, attracted to the nutrient-rich tissues of mistletoe, may impede its establishment in lower branches or smaller trees (Sessions and Kelly, 2001). All these hypotheses necessitate exploration in future studies to evaluate their impact on the localized patterning of host mistletoe association across their shared ranges.

When examining the relationship between mistletoe diameter size on host branch size, we found that larger branches hosted larger mistletoes, to the extent that they can grow given physiological constraints faced by the mistletoe due to host xylem nutrients and water movement (Tennakoon and Pate, 1996). This finding is congruent with other studies highlighting that seed establishment and survivorship correlates positively with branches of appropriate sizes that can host them, as is the case of *Phoradendron robustissimum* Eichler (Santalaceae: Santalales) on *Sapium glandulosum* (L.) Morong (Euphorbiaceae: Malpighiales) in Costa Rica (Sargent, 1995).

In conclusion, our study emphasizes the significance of plant-plant interactions by examining the impact of host availability, and host size on the dispersal, establishment, and survivorship of mistletoes. By examining the role of hosts in mistletoe presence and parasitism at local scales, we can gain insights into the broader eco-evolutionary dynamics of stem parasites among mistletoe taxa. Given that mistletoes differ in the anatomy of haustorial connections (e.g. epicortical roots, wood roses, clasping unions and bark strands) future studies should focus of how the connection influences host susceptibility and whether mistletoes differ in their branch constraints given haustorium anatomy (Calvin and Wilson, 2006). Additionally, since mistletoes are important components of plant communities globally (Hódar et al., 2018; Muche et al., 2022; Watson and Herring, 2012), comparative studies of host susceptibility across the host phylogeny will help clarify whether certain host taxa are more susceptible than others and to what extent this has influenced mistletoe's evolutionary history.

As keystone species, mistletoes play a crucial role in shaping trophic-level interactions by facilitating nutrient cycling and providing essential food sources and shelter for birds and other animal taxa, particularly during challenging environmental conditions (Hódar et al., 2018; Watson, 2001; Watson and Herring, 2012). Consequently, studies focusing on these interactions can yield invaluable insights that will greatly contribute to the development of effective conservation strategies, for these keystone species, at both local and regional scales.

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CRediT authorship contribution statement

Y. Santiago-Rosario Luis: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Espinoza-Espinoza Nicole:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft. **Gómez Quimey:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft. **Martínez de Zorzí Victoria:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft. **A. Ramírez-Ortiz Ramón:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Rodríguez Karla:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft.

Declaration of Competing Interest

The authors declare no competing interest.

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