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Standing Herbivory Is Not Affected by Tree Sex or Conspecific Density in a Dioecious Understory Tropical Tree Species

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ABSTRACT

Leaves are critical to plant photosynthesis and the loss of leaf area can have negative consequences for an individual's performance and fitness. Variation in plant defenses plays a large role in protecting their leaves from attack by insect herbivores. However, trade-offs in allocation among growth, reproduction, and defense may limit the availability of resources for any one aspect of a plant's life-history strategy, which would lead to greater herbivory in those plants that allocate more resources to growth or reproduction than to defense. Patterns of sex-biased herbivory in dioecious plants are well documented yet are known to vary in the direction (female or male) of their bias. A greater concentration of conspecifics may also increase herbivore attack through negative density dependence. In order to test the hypothesis that sex-biased herbivory varies as a function of conspecific density, we measured standing herbivory on 2350 leaves on 302 trees of the dioecious understory tree *Iryanthera hostmannii* (Myristicaceae) situated in a large forest dynamics plot in a lowland tropical rain forest in Ecuador. We found no difference in standing herbivory between the 169 male and 133 female trees, nor for focal trees surrounded by higher densities of conspecifics. The slow-growing, shade-tolerant growth patterns of *I. hostmannii* may contribute to suppressed differential expression of secondary sex characters in leaf defenses, leading to similar levels of herbivory between males and females. Considering the factors that most strongly affect herbivory in dioecious species is important in understanding the evolution of sex-related traits more broadly.

ABSTRACTA

Las hojas son fundamentales para la fotosíntesis de las plantas, así que la pérdida del área de la hoja puede tener consecuencias negativas para el desempeño y la aptitud del individuo. La variación en las defensas de las plantas juega un papel importante contra el ataque de insectos herbívoros. Sin embargo, las compensaciones en la asignación de recursos entre crecimiento, reproducción y defensa pueden limitar la disponibilidad de recursos para cualquier aspecto de la estrategia de historia de vida de una planta, lo que llevaría a una mayor herbivoría en aquellas plantas que asignan más recursos al crecimiento o la reproducción que a la defensa. Los patrones de herbivoría sesgada por el sexo están bien documentados en plantas dioicas, y se sabe que pueden variar en la dirección de su sesgo (hacia machos o hembras). Igualmente, una gran concentración de congéneres podría incrementar el ataque por herbivoría a través de un efecto negativo dependiente de la densidad. Para probar la hipótesis de que la herbivoría sesgada por el sexo varía en función de la densidad de congéneres, se midió la herbivoría acumulada en 2350 hojas en 302 árboles de la especie dioica de sotobosque *Iryanthera hostmannii* (Myristicaceae), localizados en una parcela de dinámica forestal en un bosque tropical lluvioso de tierras bajas en Ecuador. No se encontró diferencia en la herbivoría acumulada entre los 169 árboles machos y los 133 femeninos, ni en árboles focales rodeados por una mayor densidad de congéneres. El patrón de crecimiento lento y tolerante a la sombra de *I. hostmannii* puede contribuir a suprimir la expresión diferenciada por el sexo en las defensas de las hojas, lo que llevaría a similares niveles de herbivoría entre machos y hembras. Considerar los factores que más fuertemente afectan la herbivoría en especies dioicas es importante para comprender de manera más amplia la evolución de los rasgos relacionadas con el sexo.

1 | Introduction

Dioecious plants are sexually dimorphic: each individual produces either large or small gametes. Female plants produce the larger ovules (having flowers with functional carpels producing the female gametes); male plants produce the smaller pollen (having flowers with functional stamens producing pollen containing the male gametes). Because of this sexual dimorphism in gamete size, there is a differential cost of reproduction between male and female plants: in any one reproductive event, females tend to allocate more resources to reproduction than males (Lloyd and Webb 1977; Delph 1999; Obeso 2002). These different resource allocation strategies have implications for many other aspects of life-history strategies between male and female plants.

The effects of the greater investment to reproduction by females compared to males on aspects of life history can vary over time: in tropical dioecious woody plants, observed effects include more inflorescences on male trees (Queenborough, Humphreys, and Valencia 2013), larger male size (Forero-Montana, Zimmerman, and Thompson 2010), precocious male flowering (Gao, Queenborough, and Chai 2012), longer floral persistence on females (Grant et al. 2017), and greater male survival (Khanduri, Sukumaran, and Sharma 2019). These effects can be enhanced or attenuated by other factors such as phenology (Martins, Bispo, and de Paula Loiola 2021) and resource-poor versus resource-rich sites (Khanduri, Sukumaran, and Sharma 2019).

In addition to differences in life-history strategy, different plant–herbivore interactions are often observed between the sexes in many dioecious plant populations (Jing and Coley 1990; Wolfe 1997; Cepeda-Cornejo and Dirzo 2010; Rivkin, Barrett, and Johnson 2018; Johnson, Campbell, and Barrett 2015). Assuming equal resource pools between the sexes, males should have more resources available for growth and defense (Lloyd and Webb 1977; Delph 1999; Coley, Bryant, and Chapin 1985). If males prioritize allocation to growth over defense, their faster growth rates and lesser investment in chemical defenses should leave males more susceptible to herbivory than females (Ågren et al. 1999; Frazier et al. 2021; Cornelissen and Stiling 2005). Alternatively, if males prioritize allocation to defense over growth, the relatively poorly defended female plants will likely suffer greater herbivore damage than male plants (Sandoval-Molina, Lugo-García, Mendoza-Mendoza, and Janczur 2022; Maldonado-López et al. 2014; Johnson, Campbell, and Barrett 2015). The first meta-analysis in this area, largely focused on temperate species, observed the then-expected general pattern of male-biased herbivory (Cornelissen and Stiling 2005). However, an improved meta-analysis of a much-expanded dataset found no significant differences (Sargent and McKeough 2022). This broader compilation of data suggests that the basic patterns of resource allocation to reproduction, growth, and defense are likely modified to varying degrees by variation in resource availability within a plant over the seasons, and among plants in a population over spatial variation in light, water, soil nutrients, etc. (Khanduri, Sukumaran, and Sharma 2019; Martins, Bispo, and de Paula Loiola 2021). However, both meta-analyses lacked data from plants in the tropics, where herbivore–plant interactions may differ from temperate settings (Fernandes et al. 2014; Frazier et al. 2021).

The effect of insect herbivores on focal plants is likely modulated by the abundance and variety of other plants in the neighborhood (Schemske et al. 2009). A greater density of conspecific plants will likely attract more specialist insects, leading to greater herbivore pressure and more leaf area loss. In contrast, plants surrounded by few conspecifics will attract fewer specialist herbivores and suffer less leaf area loss. This idea was formally developed as the Janzen–Connell hypothesis, which predicts that higher conspecific density results in increased recruitment of host-specific natural enemies (including herbivores) (Janzen 1970; Connell 1971). These herbivores maintain diversity in plant ecosystems by reducing the survival of seedlings of abundant species and allowing rare species to succeed. The more general phenomenon is one of negative density dependence (NDD), whereby a population increasing in size attracts more pests and pathogens that have an increasingly negative effect on the individuals in the population, thereby limiting population growth. As such, variation in herbivory could clearly be driven by NDD with trees in larger groups experiencing more herbivory than isolated trees (Forrister et al. 2019).

The purpose of this study is to examine how tree sex and the local biotic neighborhood affect the standing herbivory of focal *Iryanthera hostmanii*, an evergreen, dioecious, understory rain forest tree. We tested the hypothesis that sex-biased herbivory varies as a function of conspecific density through two primary questions: (1) Do females suffer more herbivory than males? (2) Does conspecific density increase standing herbivory? The results will further develop our understanding of how variation in allocation to reproduction affects other aspects of life-history strategies.

2 | Methods

2.1 | Study Site

We conducted fieldwork in Yasuní National Park in the Ecuadorian Amazon. The park lies within evergreen lowland terra firme ever-wet forest that experiences an aseasonal climate with a mean annual rainfall of 3081 mm and temperatures that average 24°C–27°C for all 12 months (Valencia et al. 2004; Garwood et al. 2023).

Within the National Park, a 50-ha (1000 × 500 m) permanent forest dynamics plot was established in 1995. The plot is about 200 m a.s.l., but contains two ridges rising 25–40 m above the intervening valley and streams. Each 20 × 20 m quadrat in the plot was assigned a categorical habitat (ridge, slope, valley) based on median values of elevation and slope and zero convexity, using elevation estimated at each point on the grid (Valencia et al. 2004).

Within the Yasuní Forest Dynamics Plot (FDP) every tree > 1 cm diameter at breast height (DBH, 1.3 m) has been mapped, tagged, and identified (Valencia et al. 2004). About 1104 species of trees are documented in the plot (Valencia et al. 2004), including 16 species of Myristicaceae (Queenborough et al. 2007).

2.2 | Study Species

We focused our attention on one of the Myristicaceae species with a canopy accessible from the ground. *Iryanthera hostmannii* Benth. (Warb.) is a dioecious, understory tree species, 2–10 m tall, that grows mainly in wet tropical regions. Its native range is from Panama to southern Peru, Bolivia, and Brazil (Boggan, Funck, and Kelloff 1997; Hokche, Berry, and Huber 2008; Jørgensen, Nee, and Beck 2013). It has simple, alternate, evergreen leaves and a distinctive branching pattern in which whorls of branches grow out of its trunk. As with almost all Myristicaceae, it is dioecious and both males and females have similar habitat associations and growth rates, despite a male-biased sex ratio (for more details see Queenborough et al. 2007; Queenborough, Humphreys, and Valencia 2013). Within the FDP, 838 mature *Iryanthera hostmannii* trees have been identified and sexed since 2001 (Queenborough et al. 2007). Peak flowering in this species occurs in September–October and peak fruiting in January–March (Garwood et al. 2023), and phenology is synchronous between the two sexes (Queenborough, Humphreys, and Valencia 2013). In this study, we sampled from the 626 trees alive in June–August 2022, months that lie well between the peak periods of reproductive activity.

2.3 | Leaf Sampling

In July and August 2022, we sampled leaves from 302 mature *I. hostmannii* trees (133 female and 169 male), stratified from within the three different topographic habitats within the FDP (ridge, slope, and valley) (Valencia et al. 2004). At each tree, we collected eight leaves: two from each of the terminal tips of four branches (beginning with the lowest branch and counting every other, moving up and clockwise around the tree). On some larger trees, we collected four or six leaves if we could only reach two or three branches.

We calculated loss of each leaf using the software LeafByte v. 1.3.0 for image analysis (Getman-Pickering et al. 2020). Using a mobile phone, we took a photo of each leaf against a background with a reference scale that marked a 17 cm × 17 cm square. We drew the margin of any holes in the leaf to reconstruct the entire leaf. We used LeafByte to calculate the total leaf area, area lost, and area remaining. These data were used to estimate a single point-in-time value of standing herbivory for each leaf. We calculated tree-level standing herbivory by taking the mean across all leaves sampled per tree.

2.4 | Data Analysis

To test if females suffer more herbivory than males (Q1) we ran two regression models of standing herbivory (the proportion of leaf area lost) as a function of tree sex. Because proportion data are not normal and are bounded by 0 and 1, precluding the use of standard linear regression (Douma and Weedon 2019), we used a beta regression approach. The first model was a mixed-effects beta regression model at the leaf level. To enable the model to include the 68 leaves with 0 leaf area lost, we added 0.01 to every leaf, following Douma and Weedon (2019). We modeled the proportion leaf area lost of each individual leaf as a function of tree sex and tree size (DBH) as fixed effects, and individual tree as a random effect to account for the multiple leaves sampled per tree. The second model was also a beta regression but at the tree level and modeled mean leaf area lost per tree (calculating the mean across all leaves sampled per tree) as a function of tree sex and DBH (with no random effect).

To test if greater conspecific density increased standing herbivory (Q2), we modeled leaf area loss as a function of the nearby conspecific trees, in addition to tree sex and DBH. We calculated this neighborhood in two ways: (i) the number of conspecifics within 10 m of each individual focal tree, and (ii) the weighted sum of conspecifics within 10 m of the focal tree (sum[DBH/distance]; Uriarte et al. 2004). Similar to the previous analyses, we modeled herbivory (proportion of leaf area lost) using beta regression. The first leaf-level model was a mixed-effects model that included conspecific neighbors, tree sex, and size (DBH) as fixed effects, and individual tree as a random effect to account for the multiple leaves sampled per tree. The second tree-level model was a beta regression of the mean leaf area lost per tree (calculating the mean across all leaves sampled per tree) as a function of conspecific neighbors, tree sex, and DBH (with no random effect).

We included tree size (DBH) in all these models to account for the varied histories among individuals in exposure to herbivores through time and through reaching different vertical stata in the

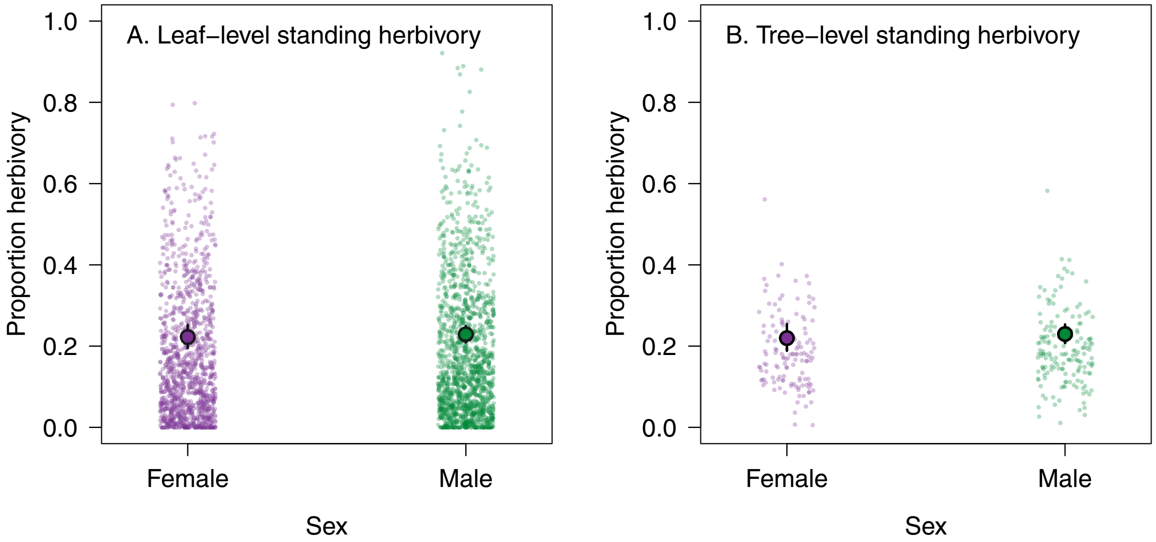

FIGURE 1 | There was no difference in standing herbivory between male and female individuals, measured on 2350 leaves from 133 female (purple) and 169 male (green) trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador). Panels show the distribution of the raw data (small pale circles) with fitted values (filled dots) for models of leaf-level (A) and tree-level (B) beta regressions. See Tables 1 and 2 for a summary of the beta regression models.

forest with age. All analyses were carried out in the statistical software environment R 4.4.0 (R Core Team 2024).

3 | Results

We estimated standing herbivory for a total of 2350 leaves from 302 trees. Mean leaf area over all sampled adult tree leaves was 74.1 cm^2 (SD = 36.2, median = 72.1, range = 8.0–228.8). Mean leaf area was similar for males (mean = 72.5 cm^2, SD = 35.5, median = 71.1, range = 8.0–228.8) and females (76.3 cm^2, SD = 37.0, median = 74.1, range = 8.7–210.4). Only 68 leaves (2.9%) had not lost any leaf area. Of the leaves that were not intact, mean area loss per leaf was 13.9 cm^2 or 19.7% (SD = 16.8%, median = 15.5%, range = 0.00970%–92.1%). Mean leaf area loss per tree was 19.1% (SD = 8.77%, median = 18.0%, range = 0.555%–58.2%). The DBH of male (mean = 48.0 mm, SD = 21.4) and female (48.5 mm, 16.0) trees was not significantly different (*t*-test: $t = 0.65$, df = 2340.1, $p = 0.516$).

3.1 | Question 1: Do Females Suffer More Herbivory Than Males?

Overall, male trees had a total of 28 uneaten leaves and 1284 eaten leaves. Of the eaten leaves, mean leaf area loss was 19.9% (SD = 17.0%, median = 15.1%, range = 1.01%–93.1%). Female trees had a total of 40 uneaten leaves and 998 eaten leaves. Of the eaten leaves, mean leaf area loss was 19.5% (SD = 16.7%, median = 14.9%, range = 0.0112%–79.8%). Contrary to our prediction, there was no significant difference in leaf area loss between male and female trees when analyzed with any of the four approaches (Figure 1; Table 1). In both models, the effect of DBH on herbivory was small but statistically significant, with larger trees experiencing slightly less standing herbivory than smaller trees (Tables 1 and 2; Figure 2).

TABLE 1 | Leaf-level standing herbivory in trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador).

Parameter	Estimate	Std. error	*z*	*p*
Female (intercept)	−1.248	0.082	−15.154	< 2e−16
Male (difference from female)	0.040	0.056	0.711	0.4768
DBH	−0.004	0.001	−2.527	0.0115

Note: Summary table of beta regression of the model herbivory per leaf as a function of Sex + DBH, using the function glmmTMB(), with family = 'beta' and link = 'logit'. AIC = −3058.0, BIC = −3029.2, logLik = 1534.0, deviance = −3068.0, degrees of freedom of the residuals = 2345. Random effect variance = 0.1366, SD = 0.3696, $N_{obs} = 2350$, $N_{groups} = 302$. See also Figure 1A.

3.2 | Question 2: Does Conspecific Density Increase Standing Herbivory? Is There Any Relationship Between Conspecific Density and Herbivory Affected by Sex?

Contrary to our prediction, there was no significant difference in leaf area loss as a function of conspecific number or weighted density (Figures 3 and 4; Tables 3 and 4). Similar to the previous set of models, the effect of DBH on herbivory was small but statistically significant, with larger trees experiencing slightly less standing herbivory than smaller trees.

4 | Discussion

Contrary to our hypotheses, we found no significant difference in herbivory between male and female trees, nor any significant effect of conspecific density or weighted neighborhood on standing herbivory in either sex. These results suggest that the greater reproductive investment of female *I. hostmannii* does not significantly affect herbivory through factors such as differential leaf growth or chemical or physical defenses between the sexes. Because *I. hostmannii* are slow-growing, shade-tolerant, understory trees, it may be that their limited-resource environment suppresses differential expression of secondary sex characters that, in turn, results in similar levels of herbivory between males and females (Liu et al. 2020; Xia et al. 2020).

4.1 | Herbivory in Males Versus Females

We found no significant difference in standing herbivory on leaves between male versus female trees, despite a widespread and comprehensive sampling of leaves and trees from the population at our site. Previous studies of sex differences in herbivory in tropical dioecious shrubs and trees have shown variable results: there are cases in which no bias was found (Leal et al. 2023; Frazier et al. 2021), cases of male-biased herbivory (Cepeda-Cornejo and Dirzo 2010; Cuda, Gillmore, and Garcete-Barrett 2018), and cases of female-biased herbivory (Sandoval-Molina et al. 2022; Maldonado-López et al. 2014).

TABLE 2 | Tree-level standing herbivory in trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador).

Parameter	Estimate	Std. error	*z*	*p*
Female (intercept)	−1.267	0.096	−13.159	< 2e−16
Male (difference from female)	0.058	0.064	0.886	0.3754
DBH	−0.004	0.001	−2.519	0.0118

Note: Summary table of beta regression of the model mean herbivory per tree as a function of Sex + DBH, using the function glmmTMB(), with family = 'beta' and link = 'logit'. AIC = −626.1, BIC = −611.2, logLik = 317.0, deviance = −634.1, degrees of freedom of the residuals = 298. See also Figure 1B.

Because *I. hostmannii* is an understory species, any difference in growth rates between male and female trees could be attenuated by the lack of available light resources in these shaded understory sites (Liu et al. 2020; Xia et al. 2020). Female and male trees of *I. hostmannii* invest similarly in flower production (measured as dry mass of flowers) and have similar growth rates (Queenborough, Humphreys, and Valencia 2013), despite the much greater investment by females in fruit (Queenborough et al. 2007), so there is some evidence that resource allocation patterns in this species may not follow the generally predicted pathways of differential investment in growth and/or defenses that might drive different amounts of herbivory between male and female trees. Alternatively, resource allocation could vary over time, with females growing slower during fruit development but investing equally into defense.

However, there is a strong bias in published studies on this topic. In a recent meta-analysis of 33 studies that examined herbivore damage to host plants of different sexes, males were found to suffer greater damage than females (Cornelissen and Stiling 2005). The majority of these dioecious species were observed in temperate ecosystems. Further, only certain temperate dioecious species (e.g., *Salix* and *Populus*) have been the focus of research on the subject of sex-biased herbivory patterns, and there is a notable dearth of research from tropical environments (Fernandes et al. 2014). This temperate bias still exists in the recent meta-analysis, despite the inclusion of a wider taxonomic sample and many more studies (Sargent and McKeough 2022). This publication bias is important because herbivore–plant interactions may differ between temperate and tropical settings (Fernandes et al. 2014; Frazier et al. 2021). Temperate plants concentrate resource allocation in spring and summer months, so herbivores have shorter periods of time in which to attack host plants. Moreover, most

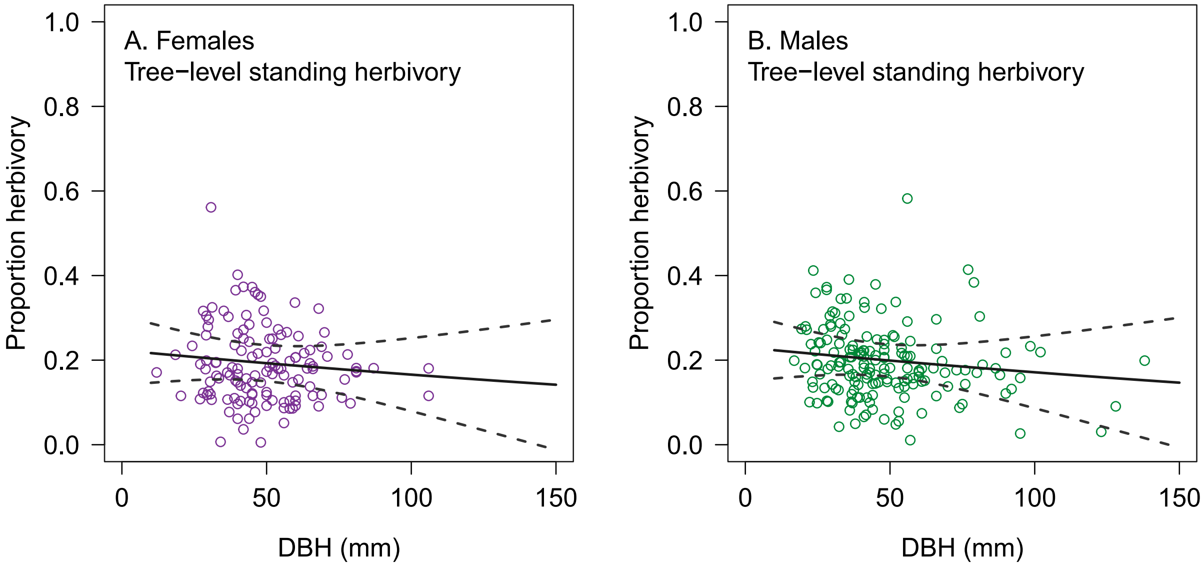

FIGURE 2 | A small negative effect of DBH on proportion mean standing herbivory at the tree level, measured on 2350 leaves from 133 female and 169 male trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador). Panels show the fitted values (solid lines) for models of tree-level beta regressions for (A) female and (B) male trees. Each dot is a tree-level mean. See Table 2 for a summary of the beta regression models.

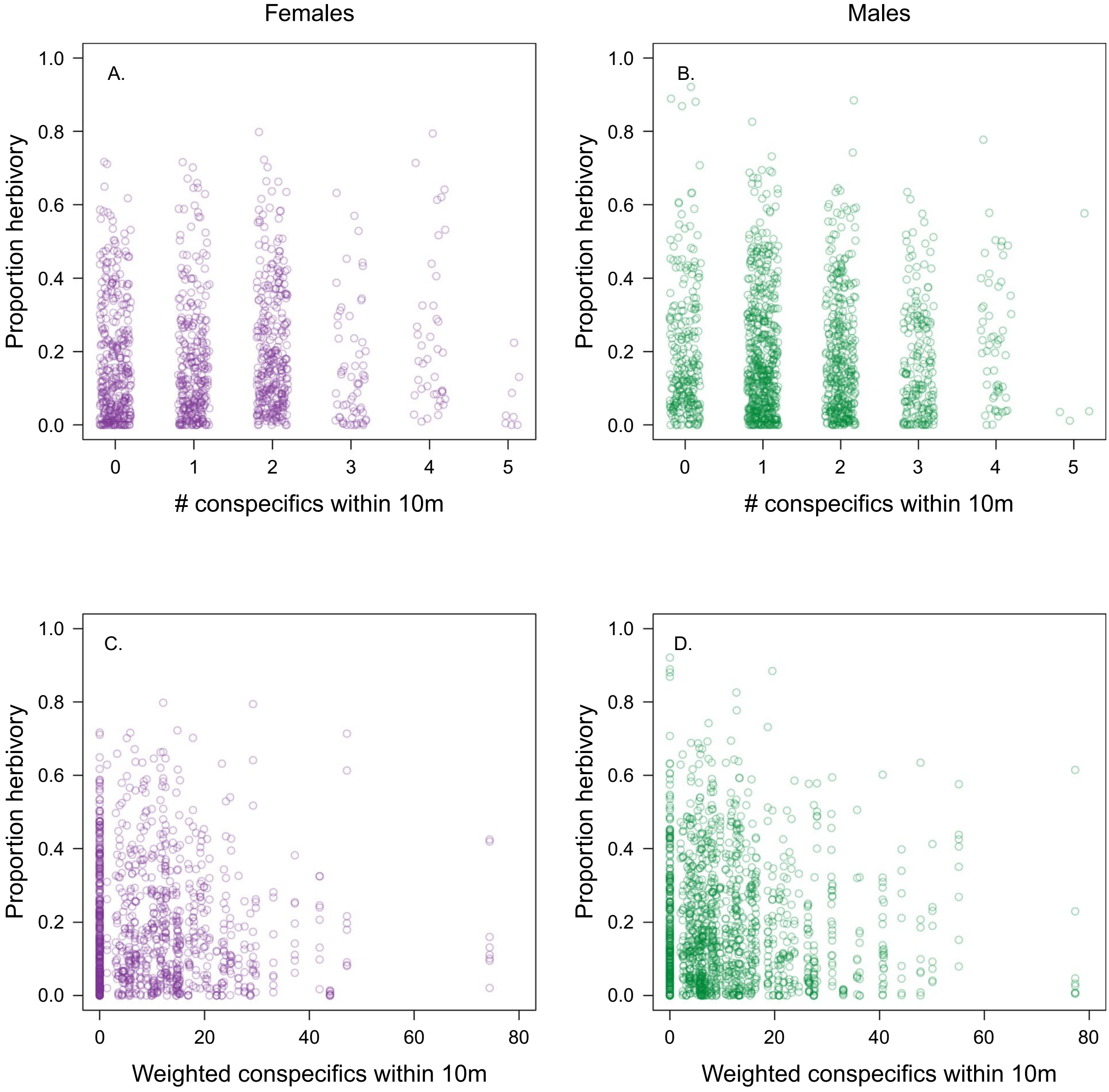

FIGURE 3 | No effect of conspecific neighbors (A, B) or weighted neighbors (C, D) on standing herbivory at the leaf level, measured on 2350 leaves from 133 female (purple, A, C) and 169 male (green, B, D) trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador). Each dot is the proportion herbivory for a single leaf. See Table 3 for a summary of the beta regression models.

temperate studies focus on damage inflicted by only one or a few herbivores, while tropical forests support greater biodiversity of herbivore fauna, and tropical host plants are likely to be attacked by a greater diversity of herbivores (Frazier et al. 2021). Future studies of sex differences in herbivory should examine a wider variety of dioecious taxa in different biomes of the tropics and subtropics.

4.2 | Effect of Conspecifics on Herbivory

Higher conspecific density tends to result in greater pressure from natural enemies leading to decreased performance (Connell 1971; Janzen 1970; Comita et al. 2014). In contrast, we found that a greater density of conspecifics did not have this effect on standing herbivory in our study species. Two factors may have led to this result. First, conspecific negative density dependence may be weaker for common species than rarer species, thus allowing common species to maintain their abundance (Mangan et al. 2010; Johnson et al. 2012). Within the plot, *I. hostmannii* is relatively common, appearing in over half (356 out of 576) of the 20 × 20 subplots, but may not be locally abundant enough to suffer from negative density dependent herbivory.

Second, the Janzen–Connell hypothesis suggests that host-specific herbivores reduce the survival of seeds, seedlings, and juvenile plants through density-dependent mechanisms (Connell 1971; Janzen 1970). Because in this study we looked only at mature trees, negative density dependence may be much weaker than that experienced at younger life stages, including in the Myristicaceae at this site (Queenborough et al. 2007).

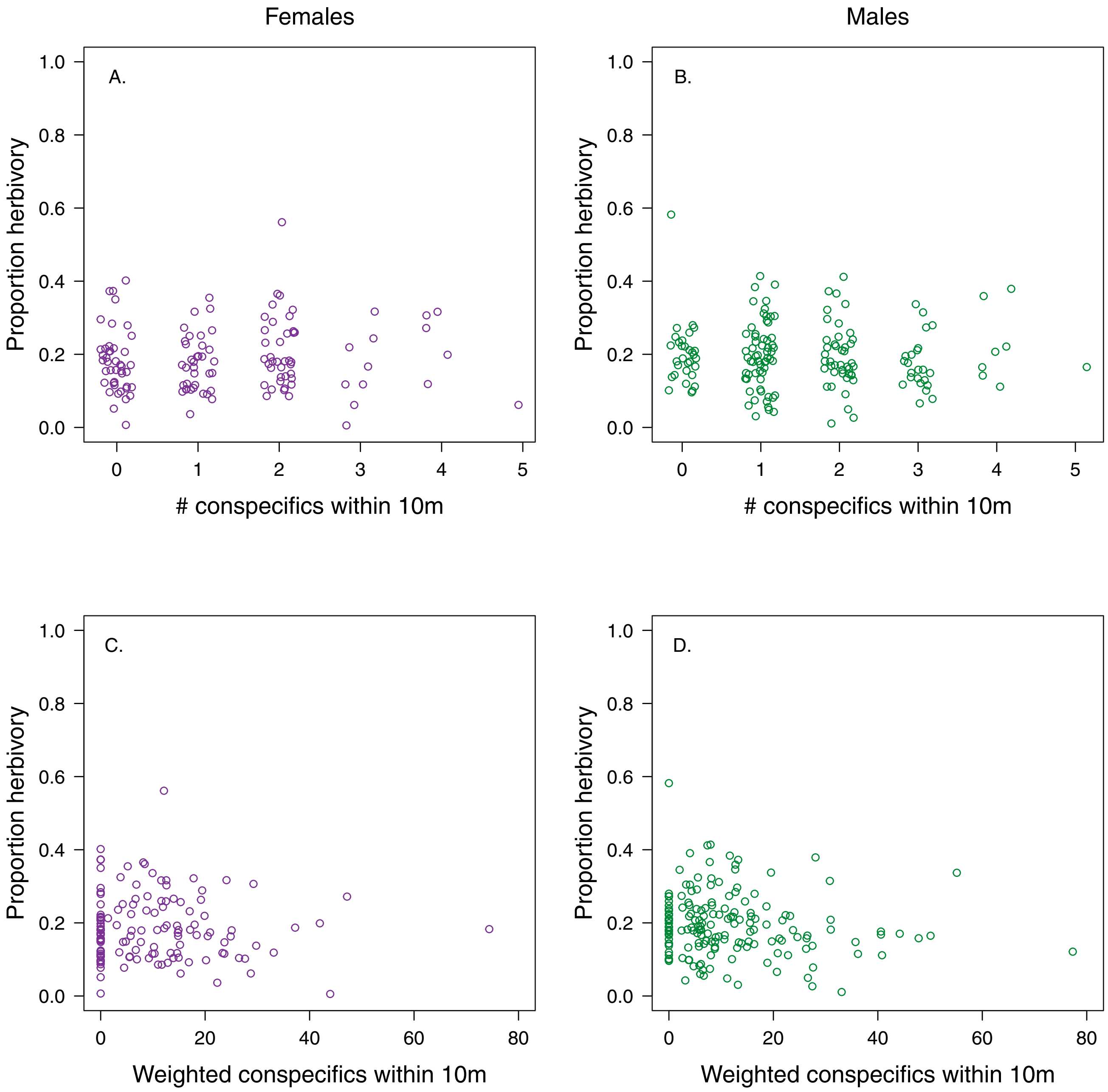

FIGURE 4 | No effect of conspecific neighbors (A, B) or weighted neighbors (C, D) on standing herbivory at the tree level, measured on 2350 leaves from 133 female (purple, A, C) and 169 male (green, B, D) trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador). Each dot is the mean proportion herbivory for an individual tree. See Table 4 for a summary of the beta regression models.

4.3 | Effect of DBH on Herbivory

Plant size (measured as DBH) had a small but statistically significant negative effect on herbivory throughout the analyses, similar to Thomas, Sztaba, and Smith (2010). These results are in contrast to the more common finding that herbivory is greater in larger trees (Shao, Zhang, and Yang 2021; Castagneyrol et al. 2019). This effect could be related to larger trees' ability to support more herbivory, since the greater number of leaves on larger trees decreases the importance of herbivory suffered by any one leaf. Greater DBH is also associated with greater height (Chen and Brockway 2017), so larger trees could potentially reach into more vertical strata and be thereby exposed to more distinct herbivores (Barone 2000; Campos et al. 2006). Larger trees may also attract greater numbers of species-specific herbivores, similar to denser patches of individuals. Studies that examine herbivory should consider the effect of plant size and how it influences exposure to herbivores.

4.4 | Overall Herbivory

Overall standing herbivory at the leaf level was high compared to other studies: only 2.9% of leaves collected were entirely intact, and mean area loss per leaf was 19.7%. In a meta-analysis, Coley and Barone (1996) found that the average annual herbivory rate

TABLE 3 | Leaf-level standing herbivory in trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador).

Parameter	Estimate	Std. error	*z*	*p*
(i) Neighborhood *N*				
Female (intercept)	−1.245	0.092	−13.59	< 2e−16
Male (difference from female)	0.041	0.057	0.721	0.471
DBH	−0.004	0.001	−2.542	0.011
# conspecifics within 10 m	0.001	0.026	0.031	0.975
(ii) Weighted neighborhood				
Female (intercept)	−1.228	0.084	−14.675	< 2e−16
Male (difference from female)	0.046	0.056	0.817	0.414
DBH	−0.003	0.001	−2.293	0.022
Weighted conspecifics within 10 m	−0.003	0.002	−1.351	0.177

Note: Summary table of beta regression of the model herbivory per leaf as a function of Sex + DBH + neighborhood, using the function glmmTMB(), with family = 'beta' and link = 'logit'. Model (i) *neighborhood N*: AIC = −3024.3, BIC = −2989.8, logLik = 1518.2, deviance = −3036.3, degrees of freedom of the residuals = 2326. Random effect variance = 0.139, std. dev = 0.3729, N_{obs} = 2326, N_{groups} = 298. Model (ii) *weighted neighborhood*: AIC = −3026.2, BIC = −2991.6, logLik = 1519.1, deviance = −3038.2, degrees of freedom of the residuals = 2320. Random effect variance = 0.1376, SD = 0.371, N_{obs} = 2326, N_{groups} = 298. See also Figure 3.

TABLE 4 | Tree-level standing herbivory in trees of *Iryanthera hostmannii* in the Yasuni forest dynamics plot (Ecuador).

Parameter	Estimate	Std. error	*z*	*p*
(i) Neighborhood *N*				
Female (intercept)	−1.248	0.106	−11.83	< 2e−16
Male (difference from female)	0.067	0.066	1.011	0.312
DBH	−0.005	0.002	−2.604	0.010
# conspecifics within 10 m	0.010	0.029	0.334	0.738
(ii) Weighted neighborhood				
Female (intercept)	−1.240	0.097	−12.782	< 2e−16
Male (difference from female)	0.071	0.065	1.092	0.275
DBH	−0.004	0.002	−2.181	0.029
Weighted conspecifics within 10 m	−0.005	0.003	−1.898	0.058

Note: Summary table of beta regression of the model herbivory per tree as a function of Sex + DBH + neighborhood, using the function glmmTMB(), with family = 'beta' and link = 'logit'. Model (i) *neighborhood N*: AIC = −613.5, BIC = −595.0, logLik = 311.7, deviance = −623.5, degrees of freedom of the residuals = 293. Model (ii) *weighted neighborhood*: AIC = −617.1, BIC = −598.6, logLik = 313.6, deviance = −627.1, degrees of freedom of the residuals = 293. See also Figure 4.

(not standing herbivory) in shade-tolerant species in the tropics was 11.1%. However, for gap specialists, the average (48.0%) was much higher. Additionally, because late-successional species tend to have longer leaf life-span, standing herbivory (representing an accumulation over time) is more likely to overestimate the annual herbivory rate of these species (Poorter et al. 2004). In light of these findings, an average standing herbivory of 19.7% in our study is probably within the expected range, although we lack data on leaf development, expansion rate, and life span in the Myristicaceae.

5 | Conclusions

We found no significant effects of conspecific density or tree sex on standing herbivory in the understory tree *I. hostmannii*. Though male-biased herbivory is often found in dioecious species, the majority of studies have taken place in temperate regions. Our study fits into an expanding body of research on tropical dioecious species showing that these taxa may not adhere to the rule of male-biased herbivory to the same extent as temperate species. Future studies of sex-biased herbivory in tropical dioecious species should diversify the species studied and use herbivory rate (rather than standing herbivory) when possible. Through these lines of study, we can better understand the factors that most strongly affect herbivory in dioecious species and the evolution of sex-related traits more broadly.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at http://doi.org/10.5061/dryad.c59zw3rk3.

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