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FACULTAD DE CIENCIAS EXACTAS Y NATURALES
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Patrones de distribución de recursos en los árboles de los jardines del diablo: Crecimiento y reproducción de la miremecofita dioica *Duroia hirsuta*

Disertación previa a la obtención del título de Licenciada en Ciencias Biológicas

SOFÍA GABRIELA MONTALVO YÁNEZ

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Certifico que la Disertación de Licenciatura en Ciencias Biológicas de la Srta. Sofía Gabriela Montalvo Yánez ha sido concluida de conformidad con las normas establecidas; por lo tanto, puede ser presentada para la calificación correspondiente.

Dr. Renato Valencia

Director de la Disertación

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A mis padres y hermana

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1 RESUMEN

Las plantas dioicas generalmente presentan variación en la distribución de sus recursos. El costo de la reproducción es usualmente considerado como el factor principal que provoca diferencias en los rasgos de la historia de vida entre los sexos. Sin embargo, factores bióticos como abióticos pueden marcar estas diferencias afectando a machos y hembras de manera diferente. **Métodos:** Se estudiaron más de 100 árboles de *Duroia hirsuta* desde el 2013 hasta 2021 para determinar las diferencias en la distribución de recursos entre machos y hembras. Se analizó la proporción de sexos, la tasa de crecimiento anual, el florecimiento y la fructificación utilizando pruebas estadísticas no paramétricas y modelos GLM. **Resultados:** La población de *D. hirsuta* está sesgada hacia los machos. Los árboles crecen de manera diferente dentro y fuera de los jardines del diablo. Los machos crecen más rápido y florecen más frecuentemente que las hembras dentro de los jardines. Nuestros resultados sugieren que las hembras presentan un mayor costo de reproducción que se vuelve evidente cuando las hormigas del género *Myrmelachista* están presentes. **Conclusiones:** Los árboles de *Duroia hirsuta* presentan dimorfismo sexual asociado a un mayor esfuerzo reproductivo de las hembras. Las diferecias entre sexos se vuelven evidentes en los jardines del diablo y afectan de manera particular a machos y hembras. A pesar de los beneficios proporcionados por *Myrmelachista*, su presencia aparenta ser más costosa para las hembras que para los machos.

Palabras clave: costo de reproducción, distribución de recursos, jardines del diablo, *Myrmelachista schummani*, Rubiaceae, trade-offs.

2 ABSTRACT

Premise: Variation in the resource allocation is expected in dioecious plants. Although the cost of reproduction is usually the main factor that leads to differences in life-history traits between the sexes, biotic and abiotic factors can accentuate these differences affecting males and females differently.

We evaluated the variation in resource allocation of the dioecious *Duroia hirsuta* tree and how the mutualistic relationship with *Myrmelachista* might affect sexes differently. **Methods:** We studied more than one hundred *D. hirsuta* trees from 2013-2021 to determine differences in the resource allocation between sexes. We analyzed sex ratio, growth rate, flowering, and fruiting using non-parametric tests and GLM models. **Results:** The population of *D. hirsuta* was male-biased. Trees grow differently inside and outside devil's gardens. Males grew faster and flowered more frequently than females in devil's gardens. Flowering and fruiting were also higher in these places. Our results suggested that females have a greater resource allocation for reproduction that becomes evident when *Myrmelachista* ants are present.

Conclusions: *D. hirsuta* trees exhibit sexual dimorphism associated with a higher reproduction cost which becomes evident inside devil's garden. The characteristics of these places might affect females and males differently, and besides the positive effects of *Myrmelachista*, the presence of these ants is more costly to females.

Key Words: Devils' gardens*; Duroia hirsuta; Myrmelachista schummani;* resource allocation; trade- offs; reproduction cost; Rubiaceae

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Title

Resource allocation patterns in the trees of Devil's gardens: Growth and reproduction in the dioecious ant myrmecophyte *Duroia hirsuta*

Author's first name, middle initial, surname

Sofía G. Montalvo[1*]

Renato L. Valencia[2]

Simon A. Queenborough[3]

Filiation and unabbreviated address.

1. Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
2. Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, Quito, Ecuador
3. Yale School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut

* sofi.8montalvo@gmail.com

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Running title

Resource allocation patterns in the trees of Devil's gardens.

In all living organisms, energy is a limited resource that is allocated towards different aspects of their life history (Obeso, 2002). In plants, energy is principally divided among vegetative growth, defense, and reproduction (Cobo-Quinche et al., 2019). Life-history theory suggests that when one aspect requires more resources, less energy is available for the others (Ashman, 1994). These trade-offs in resource allocation often lead to a negative association between the energy used for present reproduction and future processes such as growth, development of defenses, reproduction, or survival (Stearns, 1989; Ashman, 1994; Obeso, 2002). Populations of dioecious plants are a good study system, because they allow us to isolate the investment to reproduction from other aspects of life history (Obeso, 2002).

In dioecious plants, the cost of any one episode of reproduction is often different for males and females (Nicotra, 1999; Rocheleau and Houle, 2001; Obeso, 2002). Males generally invest less energy in reproduction than females because they do not produce resource-intensive fruits or seeds (Rocheleau and Houle, 2001). Because available resources are usually limited, a greater energy investment to reproduction leaves less available for vegetative growth, survival, or defense development in females (Rocheleau and Houle, 2001; Boege and Marquis, 2005). Therefore, females of dioecious species often show lower rates of vegetative growth, survival, and flowering frequency compared to males (Ataroff and Schwarzkopf, 1992; Nicotra, 1999; Wheelwright and Logan, 2004). In contrast, males tend to flower precociously and more frequently than females (Ataroff and Schwarzkopf, 1992; Allen and Antos, 1993). This differential in the cost of reproduction can produce significant differences in life-history traits between males and females in dioecious plants, including in when and where plants attain reproductive maturity (Rocheleau and Houle, 2001).

The sex ratio in dioecious plants is commonly different from the expected 1:1 population sex ratio (Field et al., 2013a). In most cases, male-biased populations are found, although female-biased populations also occur in some species (Opler and Bawa, 1978; Nicotra, 1998; Ueno et al., 2007). The effective sex ratio (i.e., the number of reproductively mature male and female individuals) in dioecious plants can be influenced by abiotic and biotic factors (Pfeiffer et al., 2019). Light, nutrient availability, and habitat quality may favor the establishment of males or females depending on their requirements (Lloyd and Webb, 1977). In females, some separation of habitat between sexes (spatial segregation of the sexes) can help to alleviate the high cost of reproduction, if they inhabit resource-rich areas (Rocheleau and Houle, 2001). Moreover, pollination and seed dispersal can also influence the sex ratio in plants. Trees with insect pollination and biotic dispersal of their seeds tend to have a higher proportion of males, while trees with the same type of pollination but abiotic dispersal tend to have a higher number of females (Sinclair et al., 2012).

The dioecious tree *Duroia hirsuta* is a myrmecophyte that can harbor diverse ant species (Báez et al., 2016), but has a particular mutualistic relation with *Myrmelachista* ants (Frederickson et al., 2005). The trees provide shelter (in the form of domatia on their branches (Kattan et al., 2008) for the ants, which in turn provide protection from herbivores. In addition, the mutualist ants also poison all plants surrounding their host tree with formic acid (Frederickson et al., 2005). Consequently, they create low diversity vegetation-free zones inhabited almost exclusively by *D. hirsuta* trees (Olesen et al., 2002; Frederickson et al., 2005). These patches, known as "devil's gardens", stand out in western Amazonian forests (Malé et al., 2020).

Báez et al (2016) found that the mutualistic relationship between ants and *Duroia hirsuta* is linked to trees' ontogeny. Small *D. hirsuta* trees that host *Myrmelachista* grew more than twice as fast as trees that did not host this ant species. However, large *D. hirsuta* trees hosting *Myrmelachista* did not show this effect; these trees performed better when they were not hosting *Myrmelachista* in devil's gardens. Hosting *Myrmelachista* seems to become costly to the plant as it grows, and it is likely more convenient to have other ant species such as *Azteca*, which are more aggressive and can provide greater protection against herbivory but do not clear the surrounding vegetation (Frederickson, 2005; Báez et al., 2016). Thus, tree ontogeny and the species of ant hosted within it both influence the benefits that *D. hirsuta* obtains from the mutualistic relationship (Báez et al., 2016).

Most investigations of *Duroia hirsuta* have covered its mutualistic interactions with *Myrmelachista* (Olesen et al., 2002; Frederickson, 2005; Frederickson et al., 2005; Frederickson and Gordon, 2007, 2009; Báez et al., 2016), leaving aside the ecological dynamics of these gardens. Further, while Frederickson (2005) made note of some trees with fruit or flowers, studies related to the reproduction and ecological differences between female and male trees of *D. hirsuta* are nonexistent. Devils' gardens do not provide just an opportunity to study the mutualistic relationship between plants and ants, but the effects that this interaction could have on the ecology of dioecious plants.

In this study we analyze a population of more than one hundred *Duroia hirsuta* trees to understand how variation in resource allocation between male and female trees can affect growth, and flower and fruit production over several years. We addressed the following questions: (1) Is sex-ratio different from 1:1 in *D. hirsuta* population? (2) Is growth rate different between males and females? (3) If so, is it higher inside devil's gardens? (4) Are females and males allocating resources differently? (5) If so, does it vary inside devil's gardens?

MATERIALS AND METHODS

Study area

Yasuní National Park is located in the northeastern part of the Ecuadorian Amazon region and has an extension of about 9820 km^2, making it the largest protected reserve in this area (Valencia, Foster, et al., 2004). The average precipitation in Yasuní is approximately 3,000 mm per year, and the average mean temperature is about 25ºC (Pérez et al., 2014). Due to the high diversity found for both plants and animals, the Park is considered one of the most biodiverse sites in the world (Pérez et al., 2014). This study was conducted in the western 25 of the 50-ha Yasuní forest dynamics plot (FDP, 0°41′ S 76°24′ W) (Valencia, Condit, et al., 2004). The FDP elevation range is 216–248 m above sea level, and it contains two ridges and one valley that flood for brief periods (Valencia, Foster, et al., 2004). Every 5 years, all stems >1 cm DBH within the FDP are mapped, marked, and measured for diameter. (Pérez et al., 2014)

Study species

Duroia hirsuta K.Schum (Rubiaceae) is an understory myrmecophyte dioecious tree of 4–10 m high (Pérez et al., 2014). The branches develop domatia, hollow structures that harbor scale insects and ants (Pfannes and Baier, 2002; Kattan et al., 2008). *Duroia hirsuta* produces white flowers and pubescent globose berries (Pérez et al., 2014). Flowering occurs from May to June and fruiting from October to November (Pérez et al., 2014). Female plants produce 2–3 flowers per inflorescence, while male plants produce about 10 flowers per inflorescence.

The ant species *Myrmelachista schummani* is typically found in these trees, even though other species such as *Azteca*, *Brachymyrmex*, *Pheidole*, and *Solenopsis* can also be present (Báez et al., 2016). When *Myrmelachista* ants are present, they form low-diversity vegetation-free zones known as "devil gardens" (Frederickson et al., 2005; Pérez et al., 2014). These gardens, dominated by *Duroia hirsuta* can contain up to 594 individuals; however, in Ecuador, the gardens studied are much smaller, having a maximum of 11 individuals (Frederickson and Gordon, 2009; Báez et al., 2016).

Field surveys

Tree growth**—**We use the tree census data from 2013 and 2021. For estimating tree growth, we used the DBH taken from individual *Duroia* during these years (DBH ≥ 1 cm). We used the growth data of 137 trees, 27 were excluded for this analysis as they presented inconsistencies in the DBH measurements.

Flowering and fruit census**—**The low number of flowers and fruits produced per tree make *D. hirsuta* a good model to study variation in resource allocation between males and females. We use data of the presence of fruits produced in 2016–2019 and presence of inflorescences in 2016–2020.

Even though devil's gardens are formed by almost only *Duroia hirsuta* trees occupied by *Myrmelachista*, comparing the censuses of 2013-2021 we found that some trees that initially had *Myrmelachista* with the pass of the years they lost these ants, and other ant species occupied these trees. According to 2021 census, 92% of the trees that were inside devil's gardens harbor *Myrmelachista,* so there was just a small percentage of trees that did not have these ants. For this reason, we assumed that all the trees found inside devil's gardens since 2013 to 2021 harbor *Myrmelachista*.

Data analysis

Sex ratios were expressed as proportions (males/females + males) and to test if they were significantly different from 1:1, we used a G-test (Wilson and Hardy, 2002). To determine if growth rate was different between males and females, we calculated the relative annual tree growth rate with the diameter measures of each individual using the formula $[(DBHt_1 / 2)^2 – (DBHt_0 / 2)^2] / [(DBHt_0 / 2)^2 \times (t)]$, t represents the time between censuses, t_1 represents the later DBH measurement, and t_0 is the initial DBH measurement (Báez et al., 2016). We used the Kruskal-Wallis test and the Kolmogorov–Smirnov test to detect significant statistical differences in the relative tree growth rate between the sexes considering several factors such as sex, ant specie, and devil's gardens. To determine if fruiting and flowering frequency and production was influenced by sex, devil's garden, or ant specie, we used a GLM (logistic regression) with a binomial and Poisson distribution.

RESULTS

The censuses held from 2013 to 2021 collected information of 291 trees of *D. hirsuta*, however only 164 could be identified as males or females. When we analyzed all *D. hirsuta* trees we found that the population was male-biased (G = 9.42, df = 1, P = 0.002). Although, when we look over the population that was inside and outside devil's gardens separately, there was not a significant deviation from the equilibrium 1:1 in the population that was outside devil's gardens (G = 2.46, df = 1, P = 0.117). Inside devil's gardens the population was still male-biased (G = 7.78, df = 1, P = 0.005; Fig. 1).

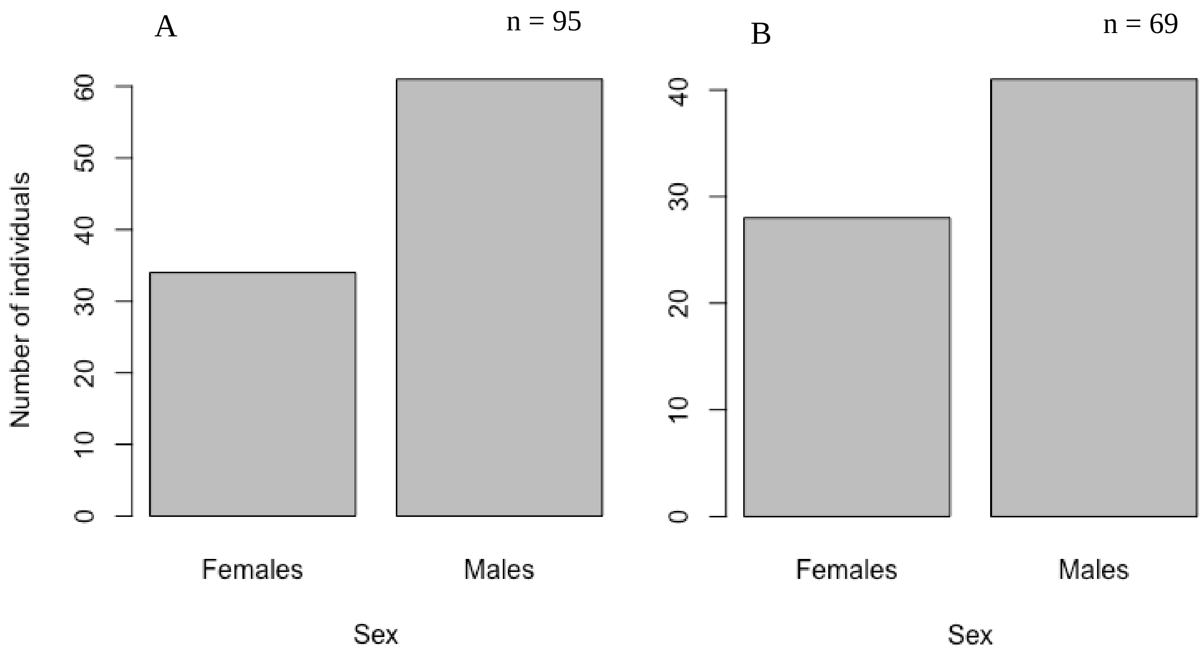

Figure 1. Number of individuals of female and male trees that were (A) inside and (B) outside devil's gardens on the Yasuní Forest Dynamics Plot.

Tree growth**—**We found 83 male and 54 female trees when examining the censuses from 2013 to 2021. There was no difference in growth rates mean between males and females (χ^2 = 3.71, df = 1, P = 0.054), however, the trees that were inside grew more than twice as much as the trees that were outside devil's gardens (mean relative growth rate 0.061 mm year^{-1} for trees inside devil's gardens vs. 0.024 mm year^{-1} for trees outside devil's gardens; χ^2 = 26.99, df = 1, P less than 0.001; Fig. 2). Additionally, we found that inside devil's gardens males grew 1.5 times more than females (mean relative growth rate 0.045 mm year^{-1} for female trees inside devil's gardens vs. 0.071 mm year^{-1} for male trees inside devil's gardens; χ^2 = 5.15, df = 1, P = 0.023; Fig. 3).

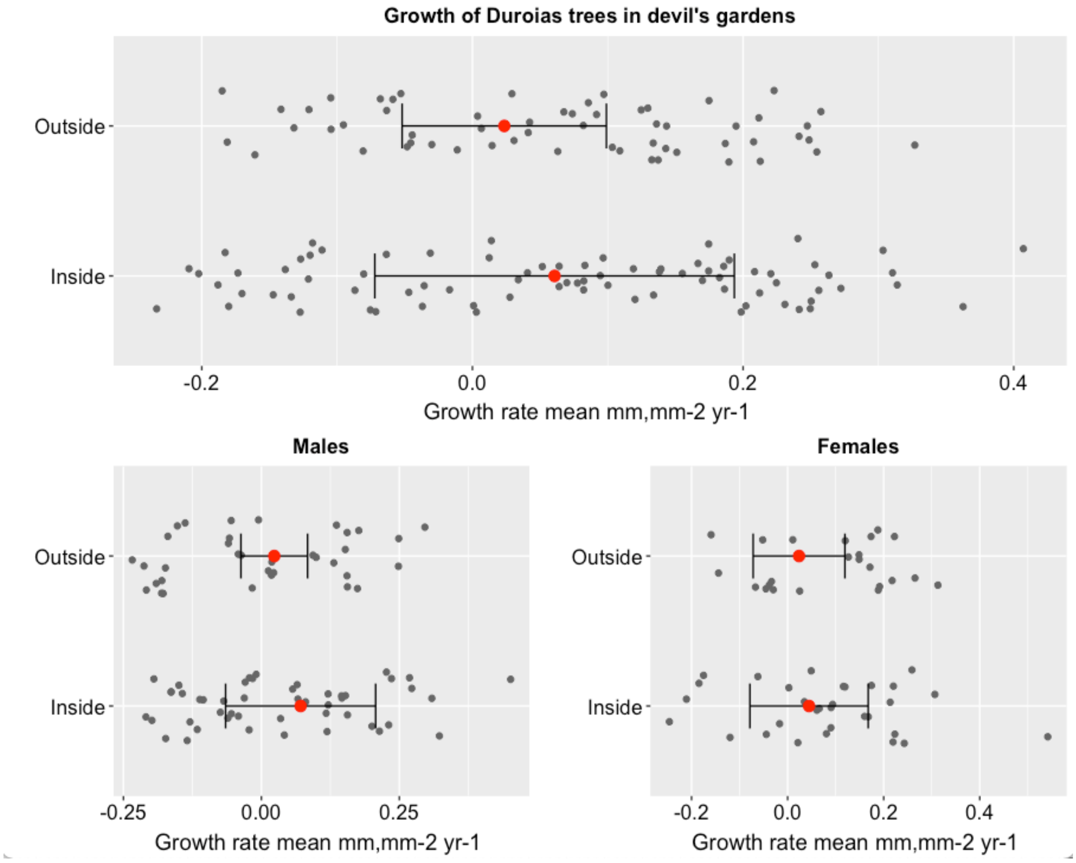

Figure 2. Growth rate of *Duroia hirsuta* trees inside and outside devil's gardens on the Yasuní Forest Dynamics Plot (DBH = diameter at breast height). Red dot = mean. Black lines = SD (standard deviation).

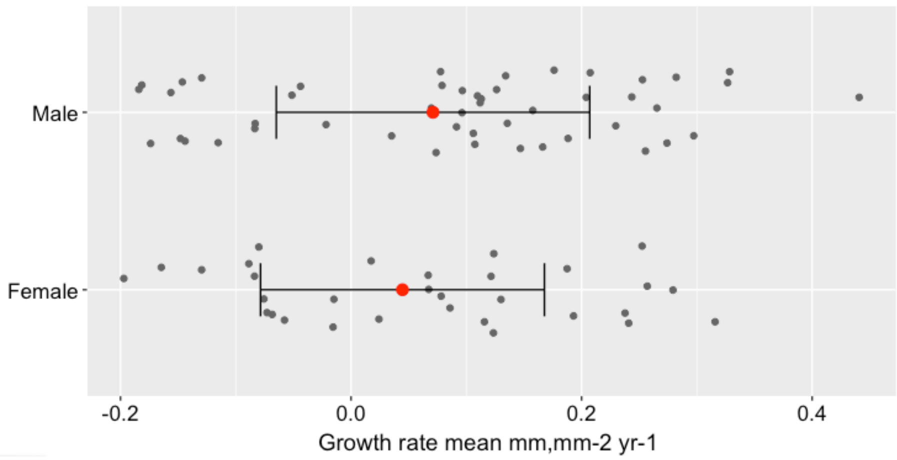

Figure 3. Growth rate of *Duroia hirsuta* male and female trees inside devil's gardens on the Yasuní Forest Dynamics Plot (DBH = diameter at breast height). Red dot = mean. Black lines = SD (standard deviation).

Flowering **—** A total of 139 trees flowered at least one time during the censuses of 2016-2020. During these five years, more males flowered than female trees (81 males, 58 females). In 2018 almost all trees flowered (93%) in comparison with 2016 (25%), the poorest year. For censuses in 2016 - 2019, tree size had a positive impact on flowering outside and inside devil´s gardens. More trees flowered as DBH increased, this did not happen in 2020, though. There were more male trees flowering than females during 2016, 2019 and 2020, however this pattern was not clear in 2017 and 2018 (Table 1). Additionally, we found that in 2018 and 2020 males produced more inflorescences than females (Table 2). Besides flowering patterns were different each year, *Duroia hirsuta* trees that were in devil's gardens always flowered significantly more frequently and produced more inflorescences than the trees that were outside (Tables 3 and 2).

Table 1. Presence/absence of inflorescences in *Duroia hirsuta* trees in the Yasuní Forest Dynamics Plot, as a function of DBH, sex and devil's garden, using generalized linear models (glm) with a binomial distribution. p = p-value (estimates in **bold** are significant). CI = Confidential intervals.

	2016			**2017**			**2018**			**2019**			**2020**		
Predictors	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*	*Odds Ratios*	*CI*	*p*
Intercept	0.00	0.00 – 0.06	**0.001**	0.08	0.01 – 0.39	**0.003**	0.26	0.02 – 2.58	0.259	0.02	0.00 – 0.13	**<0.001**	0.90	0.21 – 3.85	0.891
DBH	1.04	1.01 – 1.08	**0.030**	1.05	1.02 – 1.08	**0.001**	1.07	1.03 – 1.13	**0.005**	1.04	1.01 – 1.07	**0.005**	1.00	0.98 – 1.03	0.809
Sex (Male)	36.28	5.94 – 728.43	**0.001**	1.55	0.61 – 3.99	0.360	2.14	0.60 – 8.47	0.253	9.69	3.17 – 35.96	**<0.001**	3.55	1.48 – 8.94	**0.005**
Garden (Outside)	0.02	0.00 – 0.11	**0.001**	0.11	0.04 – 0.31	**<0.001**	0.23	0.05 – 0.89	**0.041**	0.13	0.04 – 0.40	**0.001**	0.23	0.09 – 0.55	**0.001**

Note: DBH diameter at breast height (1.3 m).

Table 2. Inflorescences production of *Duroia hirsuta* trees in the Yasuní Forest Dynamics Plot, as a function of DBH, sex and devil's garden, using generalized linear models (glm) with a Poisson distribution. p = p-value (estimates in **bold** are significant). CI = Confidential intervals.

	2016			**2018**			**2020**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
Intercept	1.71	0.28 – 9.12	0.538	14.74	13.15 – 16.50	**<0.001**	4.09	3.36 – 4.97	**<0.001**
DBH	1.00	0.98 – 1.02	0.840	1.02	1.02 – 1.02	**<0.001**	1.03	1.03 – 1.03	**<0.001**
Sex (Male)	1.47	0.53 – 6.09	0.518	2.10	1.96 – 2.26	**<0.001**	2.60	2.30 – 2.94	**<0.001**
Garden (Outside)	0.80	0.36 – 1.59	0.551	0.18	0.14 – 0.23	**<0.001**	0.19	0.16 – 0.22	**<0.001**

Note: DBH diameter at breast height (1.3 m).

Table 3. Flowering and fruiting frequency of *Duroia hirsuta* trees in the Yasuní Forest Dynamics Plot, as a function of DBH, sex and devil's garden, using generalized linear models (glm) with a Poisson distribution. p = p-value (estimates in **bold** are significant). CI = Confidential intervals.

	Flowering frequency			**Fruiting frequency**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
Intercept	1.68	1.08 – 2.59	**0.021**	2.50	0.70 – 8.84	0.157
DBH	1.01	1.00 – 1.01	0.069	1.00	0.98 – 1.02	0.697
Sex (Male)	1.54	1.16 – 2.08	**0.003**			
Garden (Outside)	0.57	0.44 – 0.75	**<0.001**	0.88	0.46 – 1.60	0.690

Note: DBH diameter at breast height (1.3 m).

***Fruiting* —**We obtained the fruit production of 21 *Duroia* trees from 2016 to 2019. We found that fruit production increased more than twice as much as in other censuses during 2019. We analyzed 19 trees which have always been inside or outside devil' gardens since 2013. Devils' gardens neither tree size (DBH) increased fruiting frequency in *Duroia hirsuta* trees (Table 3). However bigger trees and the ones that were inside devil's gardens produced more fruits than the trees that were outside these places (Table 4).

Even though devil's gardens are formed by almost only *Duroia hirsuta* trees occupied by *Myrmelachista*, comparing the censuses of 2013-2021 we found that some trees that initially had *Myrmelachista* with the pass of the years they lost these ants, and other ant species occupied these trees. In 2021 census, 92% of the trees that were inside devil's gardens harbor *Myrmelachista*, so there was just a small percentage of trees that did not have these ants. For this reason, we assumed that all the trees found inside devil's gardens since 2013 to 2021 harbor *Myrmelachista*.

Table 4. Fruits production of *Duroia hirsuta* trees in the Yasuní Forest Dynamics Plot, as a function of DBH and devil's garden, using generalized linear models (glm) with a Poisson distribution. p = p-value (estimates in **bold** are significant). CI = Confidential intervals.

	2016			**2017**			**2018**			**2019**		
Predictors	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*	*Incidence Rate Ratios*	*CI*	*p*
Intercept	1.00	0.07 – 9.24	1.000	2.27	1.15 – 4.41	**0.017**	1.57	0.55 – 4.24	0.384	10.97	7.43 – 16.18	**<0.001**
DBH	1.00	0.97 – 1.03	1.000	1.02	1.01 – 1.03	**<0.001**	1.02	1.01 – 1.04	**<0.001**	1.02	1.01 – 1.02	**<0.001**
Garden (Outside)	1.00	0.15 – 3.95	1.000	0.36	0.21 – 0.57	**<0.001**	0.29	0.12 – 0.57	**0.001**	0.12	0.07 – 0.18	**<0.001**

Note: DBH diameter at breast height (1.3 m).

DISCUSSION

Duroia hirsuta trees exhibit sexual dimorphism. Forest wide, population was male-biased, with males representing the 62% of the population. Flowering patterns were different between the sexes, males produced more inflorescences and flowered more frequently than females. Additionally, trees that were found inside devil's gardens produced more fruits and inflorescences and flowered more frequently. On the other hand, males and females grew differently inside and outside devil's gardens. Inside devil's gardens sex ratio was male biased, males were not only more numerous, but also presented a higher growth rate and flowered more frequently than females. Outside devil's gardens there was no difference in sex ratio or growth rate between sexes.

It is not well understood what are the causes that lead to sex ratio bias, but it may be related to specific life-history traits and adaptation strategies (Munné, 2015). We found that the population of *D. hirsuta* that was outside devil's gardens did not present a significant deviation from the equilibrium 1:1, however, inside devil's gardens the population was male-biased (2:1). In dioecious plants, male-biased populations are more frequently found than female-biased populations, although heterogeneity of sex ratios is also possible (Field et al., 2013a; b).

Dioecious populations can vary depending on the environmental conditions in which they occur (Field et al., 2013b). Environmental stress factors such as herbivory and competition can affect growth and performance, leading to sex-ratios biases (Pérez-Llorca and Sánchez Vilas, 2019). Although devil's gardens could be seen as advantageous places as they have been characterized for being low diversity free-vegetation zones, having less canopy cover and therefore more light (Olesen et al., 2002; Frederickson and Gordon, 2007), they are also places with high herbivory pressure (Frederickson and Gordon, 2007). The differences in the performance between the sexes are accentuated under stress conditions (Pérez-Llorca and Sánchez Vilas, 2019). Males may have a greater competitive ability, which could lead to a male-biased population inside devil's gardens.

We found no differences in growth rate between males and females, although males produced more inflorescences and flowered more frequently. Dioecious plants usually present asymmetrical allocation of resources that can produce a trade-off between growth and reproduction (Cepeda-Cornejo and Dirzo, 2010). When we analyze all *D. hirsuta* trees this trade-off was not evident. However, when we evaluate the populations of *D. hirsuta* that were inside and outside devil's gardens separately, we found that *D. hirsuta* males not only grew faster but flowered more frequently than females inside devil's gardens. Differences in the growth rate of *Duroia* trees have been reported before, due to the presence of *Myrmelachista*. Hence to their mutualistic relationship, these ants have almost triply tree growth in comparison with *Duroia* that do not harbor these ants (Báez et al., 2016). Frederickson (2005) reported that *Duroia hirsuta* that harbor *Myrmelachista* were more frequently observed fruiting and flowering than *Duroia hirsuta* that harbor *Azteca* ants. We found that trees inside devil's gardens flowered more frequently and produced more inflorescences and fruits than the trees that were outside devil's gardens.

Sexual differences of *D. hirsuta* suggest that females experiment a higher allocation of resources to reproduction. This cost of reproduction becomes evident when males and females cohabit in devil's garden. We suggest three different causes to explain sexual dimorphism in these places. First, for long-lived tropical trees it is costly to bear mutualistic ants and they may experience a reduce in growth rates (Stanton and Palmer, 2011; Báez et al., 2016). Besides, the benefits that *Myrmelachista* confers to *D. hirsuta* trees, they might be more costly to females than males. Second, the sexual differences in vegetative growth may be caused by differences in the competitive ability between sexes (Ågren et al., 1999). These differences are expected as a result of trade-offs that are associated to reproduction cost (Varga and Kytöviita, 2012). Finally, environmental conditions can cause variation in the degree of sexual dimorphism (Delph and Bell, 2008; Zhou et al., 2019). Herbivory as an environmental stressor may affect differently the performance of males and females (Liu et al., 2021).

Our results suggests that females of *Duroia hirsuta* may be experimenting a higher reproductive effort than males, specially inside devil's gardens. Although estimating the cost of reproduction in plants is difficult (Obeso, 2002), our study opens the possibility to thought that an unequal allocation of resources occurs in *D. hirsuta* trees and suggests that the mutualistic relationship of *D. hirsuta* with *Myrmelachista* ants can affect the performance of males and females differently. More studies are needed to understand the dynamics and processes occurring in devil's gardens and how different abiotic and biotic factors (herbivory) can influence in the resource allocation of males and females of *Duroia hirsuta* trees.

CONLUSIONS

Duroia hirsuta trees exhibit sexual dimorphism that can be associated to a higher cost of reproduction that becomes evident in devil's gardens. Besides *Myrmelachista* ants provides benefits to *D. hirsuta*, their presence can be more costly to females than males. Devil's gardens present biotic and abiotic factors that can affect *D. hirsuta* sexes differently.

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4. NORMAS PARA PUBLICACIÓN

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AJB requires structured abstracts for Research Articles and Brief Communications. The abstract is 250 words or fewer, written in the following structured format:

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If statistical analyses are used, include statistical values in the RESULTS, either in the text or within tables. Include the statistic value, degrees of freedom, and p-value for each result reported (e.g., for a t-test report "t = 32.41, df = 1, P = 0.03" for an ANOVA report "F5, 23 = 26.45, P less than 0.001" [note two df-values as subscripts with F]). Use P for significance, and p for probability.

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Numbers: write out one through nine unless a measurement, a designator, or in a range (e.g., four petals, 3 mm, 6 yr, 5–11 species, day 2). Use % instead of percent with numerals; no commas with four-digit numbers (e.g., 1000 instead of 1,000); 0.13 instead of .13.

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Every column must have an appropriately placed heading, with appropriate subheadings. In the body of the table, capitalize the first word of each entry (and proper nouns); do not use vertical lines between columns; indicate footnotes by lowercase superscript letters.

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