



Is Planting Trees Enough? The Effect of Different Types of Reforestation on the Offspring of *Trypoxylon (Trypargilum) lactitarse* (Hymenoptera: Crabronidae) in the Southern Amazon

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Abstract

The deforestation has led to local loss of species and important ecosystem services performed by them, causing ecological and economic losses. It is proposed that the reforestation of such areas aims to reduce those impacts. However, particularly in the tropics, little is known about the real success of different types of reforestation in the recovery of the species, and especially of the population parameters. Here we evaluated whether different types of reforestations affect *Trypoxylon (Trypargilum) lactitarse* Saussure (Hymenoptera: Crabronidae) in terms of abundance, percentage of emergence, proportion of males, fluctuating asymmetry, and foraging capacity. We compared primary forest (control) data to data collected in five different habitats: pasture, secondary forest, and tree plantations of *Teak*, *Ficus*, and a mixture of native species. The abundance of *T. lactitarse* was higher in tree plantations than in pasture. However, among the analyzed parameters, *Teak* plantation presented lower emergence percentage and the majority of individuals born were males. The emerged females in this habitat showed higher asymmetry and lower foraging capacity. *Ficus* showed lower individual abundance and mixed plantation showed lower emergence percentage, with both plantation types showing higher male emergence. On the other hand, in secondary forest, the analyzed parameters did not differ in relation to the primary forest, being the habitat more efficient in relation to those with tree planting. The changes in population parameters of *T. lactitarse* in different reforestations and particularly on *Teak* monocultures were probably attributed to indirect effects, such as low food availability and inadequate environmental conditions.

Introduction

In the last decades, the increase in agriculture and cattle ranching activities has been the main cause of the disappearance of tropical forests (Fearnside 2006, Newbold *et al* 2015). In the Amazon rainforest, thousands of hectares are lost every year and, as a consequence, many species of the flora and fauna are extinct (Gibbs *et al* 2010, Laurance *et al* 2011). Associated to these extinctions, there is the loss of

services which are important for the maintenance and stability of the ecosystem, leading to enormous ecological, economic, and social losses (Didham 1997, Fontaine *et al* 2006, Barral *et al* 2015, Mitchell *et al* 2015, Fearnside & Figueiredo 2017). Therefore, efforts are increasingly required to reduce the effects of deforestation and to promote biodiversity recovery (Padula & Silva 2005). In fact, every year, billions of dollars are spent on the conservation and recovery of biodiversity (Bueno *et al* 2013). Restoration of an environment is

an expensive intervention, and species chosen for planting in reforested areas can drive the whole ecological succession, influencing regional diversity, ecological interactions, and ecosystem services (Falcão *et al* 2015).

To evaluate the efficiency of these new reforested areas in the recovery of environmental quality, the use of species as bioindicators has proved to be a very effective tool (Edge 2005, Uys *et al* 2006, Engelbrecht 2010, McGeoch *et al* 2011). The sensitivity of some of these species to differences in resources and conditions among different habitats may prevent their occurrence (Dutra & Marco 2015). However, some of these species may colonize and persist on suboptimal habitats, even though suffering indirect effects on their populations. For these species, it is expected that the stress caused by suboptimal conditions may cause changes at the individual and population levels (Clarke 1993, Sanseverino & Nessimian 2008).

Environmental conditions and resources affected by disturbances, such as adverse temperatures, competition, and food scarcity, are known to be factors that may cause alterations in the development of the organisms during their ontogeny (Leung & Forbes 1996; Benítez 2013). One measure commonly used to assess the effect of these disturbances is the increase of the asymmetry (measured by fluctuating asymmetry, hereafter FA) that occurs in bilateral organisms (Palmer & Strobeck 1986). The increase of asymmetry reduces the fitness of the affected organisms in different ways depending on the taxon. However, regardless of the taxon, the asymmetry value found in the individuals allows us to assess the levels of stress to which they were subjected during their development (Leung & Forbes 1996; Pinto *et al* 2012). Thus, FA can be seen as a metric in the assessment of the quality of the environment for the organisms that live on it (Piscart *et al* 2005; Benítez 2013).

The variations in habitat quality quickly and strongly influence several insect population parameters, when compared to the other taxa, since they have several generations in a short period of time (Didham 1998; Pearce & Venier 2006; Nichols *et al* 2007). Among insects, the best indicator species are those that spend their whole life within the studied habitats (Clarke *et al* 1986; Camillo *et al* 1995). Thus, wasps that nest in pre-existing cavities fit perfectly as a bioindicator group because they depend on the availability of resources in the local environment to feed their offspring (Evans & Eberhard 1970; Tylianakis *et al* 2005). Additionally, this group is easily sampled using trap nests (Coville 1982), a method that ensures that these species actually inhabit the studied region, thus excluding those that are just passing through (Camillo *et al* 1995).

Known as spider predators, *Trypoxylon* (*Trypargilum*) *lactitarse* Saussure, 1867 (Crabronidae), is considered frequent in trap nests (Beyer *et al* 1987, Morato & Campos 2000, Buschini *et al* 2006, Araujo *et al* 2017), being more

abundant in forested environments, but also occurring in deforested areas (Buschini & Wolff 2006). This species is widely distributed from southern Argentina to southern Canada (Coville 1981). Adults use floral resources (pollen and nectar) as energy source, contributing to the pollination of various plant species (Bohart & Menke 1976). However, they also are effective as predators of several species of spiders that are consumed as primary food source during the larval development (Camillo & Brescovit 1999; Buschini *et al* 2008).

As in most of the Hymenoptera, these insects present a haplodiploid system, where unfertilized eggs give rise to males and the fertilized ones give rise to females (Crozier & Pamilo 1996). Due to their ability to control the spermatheca, females are able to choose the sex of each offspring at the moment of oviposition (Godfray 1988, Shintarou & Takayoshi 1999). In addition, there is strong evidence that females are able to adjust the sex ratio of their offspring as a function of environmental conditions (Charnov 1982). In *Trypoxylon*, one of the main characteristics associated with sexual dimorphism is body size, where females are larger than males and require greater amount of food (Buschini 2007). With this, the availability of resources may be a factor that affects the proportion of the sexes within its offspring (Morato & Campos 2000). Like other solitary wasp species, all food necessary for the development of the larva to adult stage is offered at only once (Molumby 1997, Strohm & Linsenmair 1999). Thus, insufficient food supply at the time of building their breeding cells may lead to stress during offspring development, resulting in an increase in FA of their structures (Niemi & McDonald 2004; Sanseverino & Nessimian 2008). In flying animals, this stress can lead to symmetrical differences in their wings which reduce the ability and aerodynamics of the flight, influencing its adaptive value (Swaddle 1996).

In this study, we evaluated the efficiency of different types of reforested habitats in the recovery of important parameters necessary for the maintenance of the *T. lactitarse* population in Southern Amazon. We specifically tested whether (1) the abundance of individuals, (2) emergence percentage, (3) proportion of males, (4) foraging capacity, and (5) fluctuating asymmetry are influenced by the habitat type in the recovery process when compared with primary forest.

Material and Methods

Study area

We conducted the fieldwork at São Nicolau farm (9°48'S and 58°15'W), located in the municipality of Cotriguaçu in the north of Mato Grosso State, Brazil. The farm has 10,000 ha,

of which 7000 ha are primary forest, 500 ha are secondary forests, 1700 ha are different types of reforestation, and 300 ha are pastures used by cattle. Reforestations and secondary forests were both previously pasture before the re-vegetation, which occurred between 1999 and 2000 (Rodrigues *et al* 2011). The regional climate is AW type, according to the Köppen classification (warm and humid), with an average annual temperature of 24°C, 85% humidity, and 2300 mm of precipitation (Rodrigues *et al* 2011). In this study, we collected data in five different habitats: (1) primary forest (PF) (control), defined as a “terra-firme” and closed-canopy forest without the influence of seasonal flooding of larger rivers. The understory is highly biodiverse, relatively open with a canopy height varying between 30 and 40 m with some trees reaching up to 50 m high; (2) secondary forest (SF), natural restoration without the presence of cattle or anthropogenic interference. The understory of secondary forests is extremely dense, with vegetation higher than 5 m; there is a low leaf litter accumulation and light incidence; (3) teak reforestation (TF) in monodominant stands of the exotic *Tectona grandis* (Verbenaceae), characterized by an open understory, deciduous leaf-fall pattern in the dry season, and deep leaf litter accumulation; (4) ficus reforestation (FR) in monodominant stands of the native *Ficus maxima* (Moraceae), sourced from local seed provenance, and characterized by a mixed-age understory shrubs, low leaf litter accumulation, and some patches of grasses; (5) mixed reforestation (MP) of planted native tree species, including *Tabebuia chrysotricha* (Bignoniaceae), *T. roseo-alba*, *T. impetiginosa*, *Cedrela fissilis* (Meliaceae), *Cordia alliodora* (Boraginaceae), *Simarouba amara* (Simaroubaceae), *Spondias mombin* (Anacardiaceae), *Hevea brasiliensis* (Euphorbiaceae), and *Schizolobium amazonicum* (Fabaceae), with an understory of low shrubs and grasses, and low leaf litter accumulation; (6) pasture (PT), dominated by planted grasses (not more than 50 cm tall) used as food for cattle, with very high light incidence, almost no woody vegetation and an absence of leaf litter accumulation (Rodrigues *et al* 2011). Pasture was used in our design as a “starting point” of forest succession under different reforestations.

Sample design

To sample *T. lactitarse* individuals, we used 10 sample units for each habitat, except for primary forest ($n = 14$; Fig 1). The minimum distance between each sampling unit of the same treatment was 500 m. In each sample unit, we marked five equidistant points at a distance of 50 m and installed blocks of wood up to 1.5 m high. The wooden blocks were composed of 40 holes distributed equally between the diameters 0.8, 1.2, 1.6, and 2.0 mm by 10 cm deep, where we inserted tubes of black paperboard (Camillo *et al* 1995), totaling 320

blocks and 12,800 trap nests. We inspected the traps every 20 days between August 2016 and July 2017, and those occupied were collected and replaced by another trap with the same measurements. In the laboratory, the trap nests brought from the field were placed in test tubes, closed with cotton, and kept in a dark room at temperatures of between 20°C and 25°C until the emergence of adults. Then, we pinned the emerged adults, quantified the number of cells built, identified their sex, and performed the measurements of wing load (to evaluate the foraging capacity) and fluctuating asymmetry. Voucher specimens were deposited in the Invertebrate Collection of the Universidade Federal de Mato Grosso.

Morphometric measurements

To perform the morphometric measurements of *T. lactitarse*, we randomly choose only one individual of each sex for each nest that emerged adults, totaling 119 specimens: PF (male = 10; female = 17), SF (male = 10; female = 18), TR (male = 10; female = 12), FR (male = 10; female = 12), MR (male = 10; female = 10). Due to the low number of individuals that emerged in PT ($n = 2$, Table 1), it was not possible to include this habitat in the morphometric analyses. To evaluate the fluctuating asymmetry (FA) of individuals, we removed the pair of forewings and photographed and measured the length of each wing with the aid of the software Leica Application Suite version 2.0. The length of the forewing measure starts at the beginning of the costal vein and runs up to the most apical point of the wing. We evaluated the foraging capacity of individuals based on the wing load (WL) represented by the body dry mass (DM) divided by the wing's area (WA). This metric is considered a good predictor of winged individuals' flight capacity (Polidori *et al* 2013). We measured DM with a precision balance of 0.1 mg and the area of the forewing using the software ImageJ version 1.51n. We calculated WL using the formula $WL = DM/WA$.

Data analysis

We used generalized linear mixed models (GLMM's) to determine if the abundance, emergence percentage, and proportion of males of *T. lactitarse* differ between primary forest (control) and the habitats studied. For this, we used abundance of individuals, emergence percentage, and proportion of males as response variables. As an explanatory variable (fixed effect) of the model, we used the type of habitat. Considering that we performed repeated measures at each habitat, we used sites as a random effect for all models, since each replicate was visited 12 times (Crawley 2007). For GLMM's implementation, we used the glmmTMB package, and the selection of the best model was given by the comparison using Akaike information criterion.

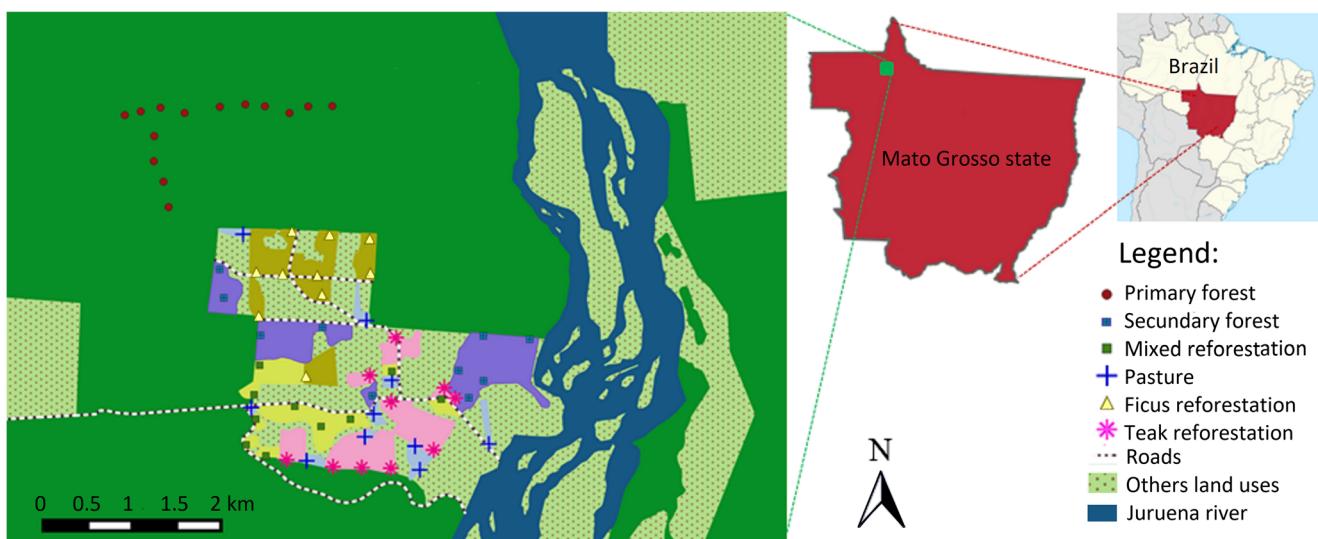


Fig 1 Map showing the spatial arrangement of our 64 sample units established in six different habitats at the São Nicolau farm, municipality of Cotriguá, State of Mato Grosso, Brazil.

We used generalized linear models (GLM's) with Gaussian distribution to determine whether FA and WL varied between habitats. As explanatory variables, we used habitats and the sex of the individuals measured. To verify if the sex of the individuals influenced the response variables within each habitat, we also added to the models the interaction between sex and habitat. After performing the GLMs, we performed the planned comparisons analysis in order to determine if the values of FA and WL (response variables) were different between primary forest and each habitat type. The planned comparison performed for FA and WL was performed separately for each sex. All analyses were performed in program R version 3.5.1 (R Core Team 2018).

Results

During the study period, we collected a total of 839 cells (368 nests) of *T. lactitarse* in the 64 sample units.

The number of cells was highly correlated with the number of nests (Pearson's $r=0.95$, $p<0.001$, $n=64$). Among habitats, PT and FR showed lower abundance of individuals in relation to PF (control), ($Z=-3.727$, $p=0.000$, and $Z=-2.460$, $p<0.01$, respectively). For habitats TR, MR, and SF, no significant differences were found (Fig 2).

The emergence percentage of *T. lactitarse* in the TR, MR, and PT was lower than PF ($Z=-2.066$, $p=0.038$, $Z=-4.186$, $p<0.001$ and $Z=-2.043$, $p=0.041$, respectively). The emergence average in PF was 51.94% of the cells, while in TR 40.21% of the cells built had emerged adults. In MR and PT, the emergence percentage was only 28.74% and 20%, respectively. The emergence percentage of SF and FR did not differ in relation to PF, with 61.18% and 50.53% of individuals born, respectively.

In relation to proportion of males, TR presented the highest deviation, 75.8% of the individuals born were males, followed by FR and MR, with 69.5% and 57.8%,

Table 1 Description of the number of cells built, emergence percentage, proportion of males and females of *Trypoxylon (Trypargilum) lactitarse* individuals born in the habitats studied (mean \pm standard error). Statistical values represent the results of planned sex ratio comparisons between pasture (PT), teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), and secondary forest (SF) with primary forest (PF).

Environments	No. of cells built	Emergence (%)	Males born (%)	Female born (%)
PT	$1.0 \pm 0.55^*$	$13.33 \pm 10.89^*$		
TR	16.2 ± 3.57	$40.20 \pm 2.25^*$	$75.81 \pm 2.33^*$	24.19 ± 3.45
FR	$6.4 \pm 1.99^*$	50.53 ± 5.91	$69.57 \pm 4.43^*$	30.43 ± 6.27
MR	9.9 ± 3.09	$28.74 \pm 2.07^*$	$57.81 \pm 6.45^*$	42.19 ± 8.96
SF	12.6 ± 3.43	61.18 ± 1.90	49.31 ± 4.85	50.69 ± 4.79
PF	9.4 ± 2.03	51.94 ± 0.51	43.42 ± 5.54	56.58 ± 4.69

*Coefficients are significantly different from zero ($p<0.05$).

respectively. The habitats with the lowest proportions of emerged males were SF (49.31%) and PF (43.42%). When comparing the proportion of males between habitats studied and PF, those actively reforested showed significantly higher values (TR: $Z = 3.421$, $p < 0.000$; MR: $Z = 2.468$, $p < 0.013$; FR: $Z = 2.362$, $p < 0.018$) (Fig 3, Table 1). Due to the low number of emergences in PT ($n = 2$), this habitat was excluded from the analysis.

The FA of the forewings differed among *T. lactitarse* individuals from the different habitats ($F_{5,118} = 7.222$; $p = 0.0001$). This asymmetric difference was also associated with the sex of the individuals ($F_{1,113} = 4.560$; $p = 0.029$). In fact, in all habitats studied, the emerged individuals showed a certain degree of asymmetry in the length of their wings. However, the lowest asymmetry was observed in the PF. In the planned comparisons, we could observe that the females born in the TR presented greater asymmetric variation than the females born in PF ($F_{1,64} = 27.589$; $p < 0.000$). In the case of males, no differences were observed between the different treatments in relation to the PF (Fig 4, Table 2).

T. lactitarse emerged individuals also differed in WL among habitats ($F_{5,118} = 3.455$; $p = 0.002$). This difference was associated with sex ($F_{1,113} = 37.100$; $p < 0.001$) and the variation between sexes was different among habitats ($F_{3,112} = 9.935$; $p < 0.001$). In PF, while males on average presented the lowest WL values, the females showed WL values close to the highest values recorded for all other habitats (Fig 5). This dimorphism in WL was also observed in MR and SF. Although a similar pattern was observed in FR, this dimorphism was less pronounced. Additionally, in TR, the opposite was found, females and males collected in this habitat presented the lowest and highest values of WL, respectively. When compared with PF, these differences were significant (Fig 5, Table 2).

Discussion

Although *T. lactitarse* is considered a species of great plasticity, potentially occupying different environments (Pérez-Maluf 1993, Buschini *et al* 2006, Oliveira-Nascimento & Garófalo 2014, Araujo *et al* 2017), the different types of habitats studied strongly influenced their nesting behavior and parameters that influence the population structure of their next generation. Biological and structural changes occurring in altered environments may have direct effects on resident species (Morato 2001; Abrahamczyk *et al* 2011). In the present study, we showed that *T. lactitarse* occurs and builds nests in all habitat types studied. In all types of tree plantations, *T. lactitarse* abundance was higher than that in pasture. However, the highest abundance of *T. lactitarse* occurred in primary forests, probably due to the greater availability of resources and less variation in the environmental conditions in this environment. The lack of vegetation cover and a microenvironment that controls the

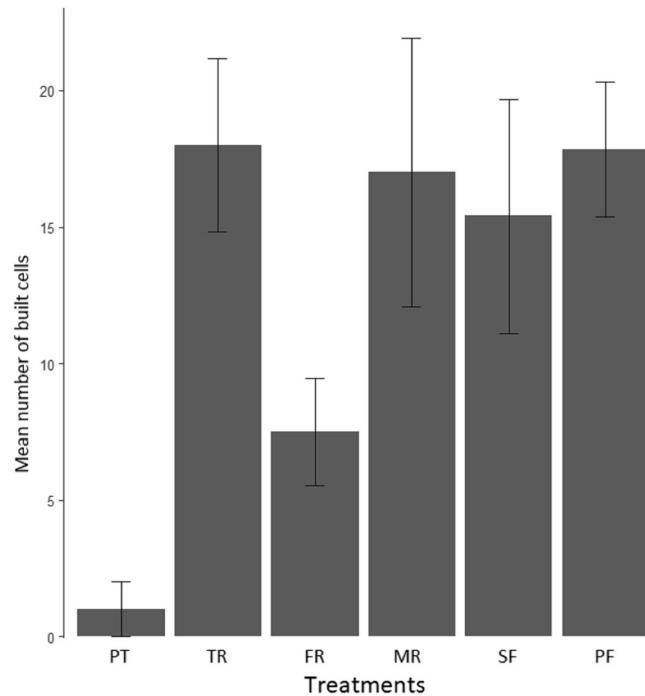


Fig 2 Mean number of cells built by *Trypoxylon (Trypargilum) lactitarse* among habitats studied in the southeast of the Amazon: pasture (PT), teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), secondary forest (SF), and primary forest (PF).

variation and amplitude in daily temperature was possibly the cause of the low occurrence and high mortality of *T. lactitarse* in pastures. These characteristics are possibly ensured by the

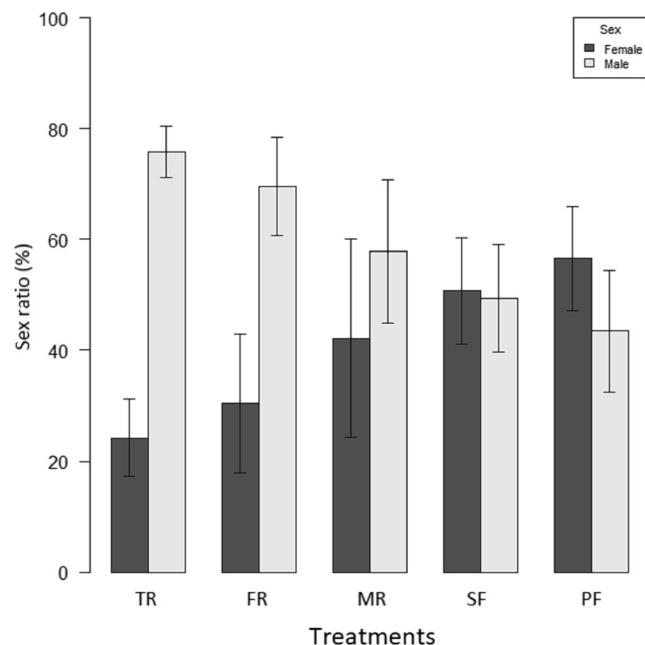


Fig 3 Sex ratio of individuals of *Trypoxylon (Trypargilum) lactitarse* born in the habitats studied in the southeast of the Amazon: teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), secondary forest (SF), and primary forest (PF).

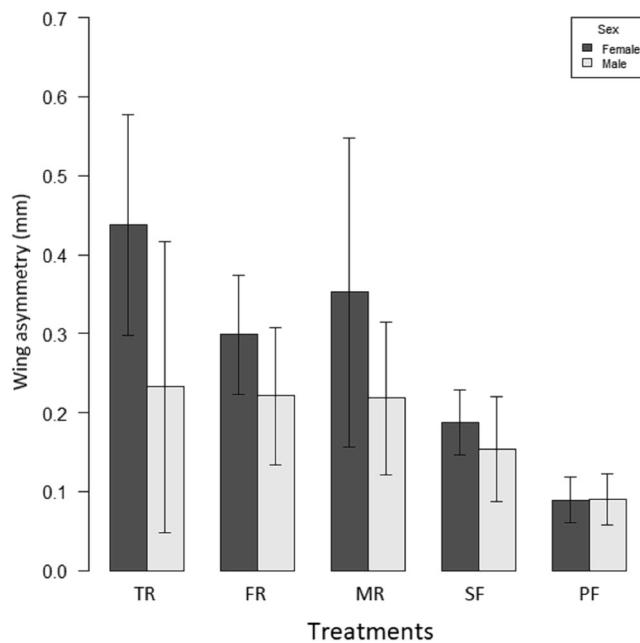


Fig 4 Asymmetric variation in the length of the posterior wings of males and females of *Trypoxylon (Trypargilum) lactitarse* among habitats studied in the southeast of the Amazon: teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), secondary forest (SF), and primary forest (PF).

intensive cattle grazing that hinders the establishment of other species of plants other than grasses (Kurn *et al* 1994, Klein *et al* 2002, Dunne *et al* 2011, Tscharntke *et al* 1998). The species preference for forested environments has also been observed in other studies (Buschini & Wolff 2006; Araujo *et al* 2017).

Although considered generalist, *T. lactitarse* appears to be more flexible in areas with higher prey availability (Buschini *et al* 2008). Spiders commonly predated by *Trypoxylon* usually live on plants where they hunt and breed (Uetz *et al*

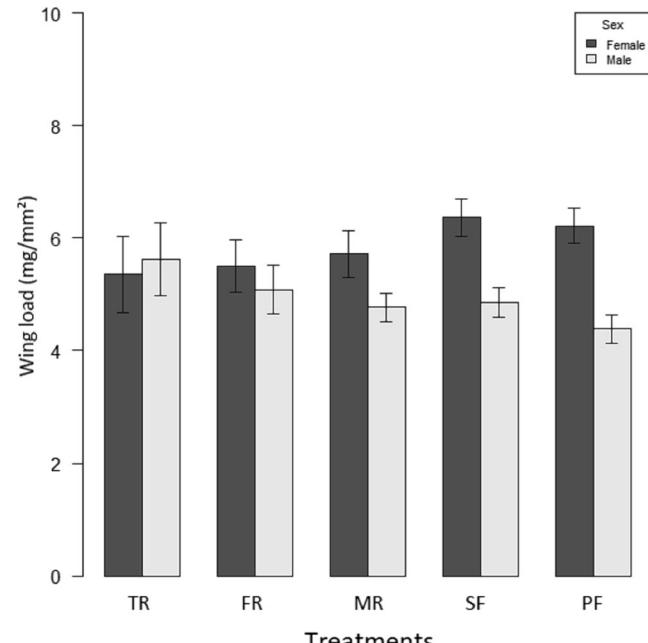


Fig 5 Variation in wing load of *Trypoxylon (Trypargilum) lactitarse* males and females emerged in the habitats studied in the southeast of the Amazon: teak reforestation (TR), ficus reforestation (FR), mixed reforestation (MR), secondary forest (SF), and primary forest (PF).

1999, Buschini *et al* 2010, Pitilin *et al* 2012). So, the prey scarcity may also contribute to the low colonization success in the pasture. In studies with other solitary Hymenoptera, spider-hunting wasps have been positively correlated with the complexity of the studied environments (Klein *et al* 2002, Loyola & Martins 2008, Steffan-Dewenter & Tscharntke 2002, Araujo *et al* 2017). This is possibly related to their low dispersal capacity, and due to their specialization in food types, nesting sites, and materials requested for

Table 2 Description of the asymmetry in wing length and wing load of *Trypoxylon (Trypargilum) lactitarse* individuals born in the habitats studied (mean \pm standard error). The statistical values represent the results of the planned comparison test of these variables for the male and female individuals born in reforestation in relation to the primary forest.

Environments	Sex	Wing asymmetry (mm)			Wing load (mg/mm ²)		
		Mean \pm SE	F value	p value	Mean \pm SE	F value	p value
TR	Female	0.44 \pm 0.06	27.59	0.0001*	5.3 \pm 0.33	13.25	0.0001*
	Male	0.23 \pm 0.09	2.892	0.0959	5.6 \pm 0.32	16.57	0.0001*
FR	Female	0.29 \pm 0.03	0.273	0.6032	5.5 \pm 0.21	2.45	0.1214
	Male	0.22 \pm 0.04	0.648	0.425	5.0 \pm 0.23	0.653	0.4232
MR	Female	0.34 \pm 0.10	3.461	0.0674	5.7 \pm 0.20	1.083	0.3018
	Male	0.21 \pm 0.04	0.949	0.3353	4.7 \pm 0.12	0.64	0.4279
SF	Female	0.18 \pm 0.02	1.872	0.176	6.3 \pm 0.13	0.373	0.5432
	Male	0.15 \pm 0.03	0.705	0.4055	4.8 \pm 0.16	0.653	0.4232
PF	Female	0.08 \pm 0.01	—	—	6.2 \pm 0.15	—	—
	Male	0.09 \pm 0.01	—	—	4.3 \pm 0.12	—	—

*Coefficients are significantly different from zero ($p < 0.05$).

nesting (Gathman & Tscharntke 2002, Steffan-Dewenter & Tscharntke 2002, Buschini *et al* 2008, Zurbuchen *et al* 2010). This suggests that all tree plantation types at least favored the colonization of *T. lactitarse* at local scale and, at the same time, the transformation of forests into structurally simple environments such as pastures may lead to its local extinction.

Even though TR presented high *T. lactitarse* nesting rates in trap nests in relation to other reforestation types, TR did not prove to be adequate for the recovery of the species population patterns observed in PF. This habitat type presented greater mortality of immatures and male-biased sex ratio for individuals born. At the same time, although FR and MR did not show difference in birth rates in relation to PF, they also showed male-biased sex ratio for the emerging offspring. The sex ratio deviation for *Trypoxyylon* species has also been recorded in other studies (Assis & Camillo 1997, Shintarou & Takayoshi 1999, Buschini 2007, Oliveira-Nascimento & Garófalo 2014, Buschini & Bergamaschi 2014). This feature has important consequences for individual fitness and population persistence and may occur in response to variations in environmental conditions, such as low food availability (Hamilton 1979, Molumby 1997, Shintarou & Takayoshi 1999). The sex-biased offspring during the nesting process may occur when there is a strong size dimorphism between sexes (Fisher 1958). Among *Trypoxyylon*, males are noticeably smaller and thus require less investment in food resources for their full development (Buschini *et al* 2010). Thus, although tree plantations favored the local *T. lactitarse* occurrence in relation to pasture, a suboptimal availability of food resources may have led the females to invest in a male-biased offspring (Krombein 1967, Sheldon *et al* 1998, Polidori *et al* 2013). Another explanation for the smaller number of females in these environments is the difference in mortality between the sexes (Brockmann & Grafen 1992). Since the resource used by one individual is not available to the other (Buschini *et al* 2010), the lack of sufficient food for the female offspring may have increased its mortality in these environments. As this is a pattern observed at local scale (site), the low availability of females has a negative impact at the population level, reducing mating and nesting rate. This reduces the persistence of *T. lactitarse* in the planted forests (Hardy *et al* 1998, 2000, Nunney & Luck 1988). Alternatively, the local persistence of species can be dependent on constant immigration of female individuals from like primary forest.

Among the habitats studied, the individuals of *T. lactitarse* emerged on SF presented morphological patterns more similar to the ones emerged in PF. In tropical environments, forest recovery in abandoned agricultural land can be very fast in the case of low-intensity land use (Chazdon 2003). Soil fertility and the presence of nearby forest remnants are also

factors that facilitate and accelerate the recovery of these environments (Guariguata & Ostertag 2001). In the Western Amazon region, pastures with less than 8 years of abandonment already had tree species growing (Uhl *et al* 1988). All the habitat types of the present study are surrounded by an extensive area of primary Amazon rainforest. Such vast source of propagules should decrease the restoration time on abandoned pastures, creating habitats richer in resources to *T. lactitarse* than reforested sites.

Although studies suggest that in the haplodiploid species of Hymenoptera the diploidism is able to reduce the effects of the stress in function of heterozygosity (Clarke *et al* 1986, Tomkins & Kotiaho 2001, Miklasevskaja & Packer 2015), our study shows that females (diploids) were more asymmetric than males. In addition, the variation in asymmetry of females emerged in TR was higher in relation to the ones emerged in PF. Curiously, males show no significant variation between habitats. Environments with some type of restriction may impose difficulties to the establishment of colonizing species, promoting low heterozygosity due the high rates of inbreeding (Mitton & Grant 1984). Therefore, individuals and populations with low heterozygosity are sensitive to disturbances during their development (Clarke 1993; Tomkins & Kotiaho 2001). This suggests that although *T. lactitarse* females are able to nest in TR, this habitat may exert pressures on the quality of their offspring. So, synergistically with the male-biased populations, the habitat can also negatively affect the quality of females born. We believe that these values were less accentuated for males by the fact that they needed fewer resources for their development. Thus, in a resource-deficient environment, females are more susceptible to development problems than males, which may account for the greater male birth in habitats like TR, MR, and FR.

The effect of environmental stress on the FA increase of organisms has been already reported in several groups, such as other insects (Chang *et al* 2007, Pinto *et al* 2012, Banaszak-Cibicka *et al* 2018), birds (Vangestel *et al* 2011), crustaceans (Ho *et al* 2009), fishes (Vandenbussche *et al* 2018), and plants (Lobregat *et al* 2017). The asymmetric differences, as observed between the wings of the *T. lactitarse* females in TR, potentially affect their adaptive success (Swaddle 1996). The disparity in these structures decreases the capability to escape from predators by reducing the efficiency in take-off and maneuverability (Tomkins & Kotiaho 2001), as well as reducing foraging abilities (Swaddle *et al* 1997; Samejima & Tsubaki 2010). A study on parasitic wasps (Bennett & Hoffmann 1998) showed that the asymmetry of the wings was negatively associated with the ability to find the eggs of the host (Lepidoptera). In addition, the impairment of foraging abilities may affect the female's fitness during the nesting process (Thomas 1993). Therefore, even though adults build nests with relatively high abundance, the females of

T. lactitarse populations born in TR are particularly more asymmetrical, decreasing the potential of population persistence on such habitats.

Females born in TR also differed in WL relative to the females emerged in PF. A lower WL reflects greater flight efficiency, since they have larger wings in relation to the body (Polidori *et al* 2013). This feature may have favored the success in the occupation of this reforestation by the founding females. We just measured the WL of the females born in TR, not the adult ones. However, if WL is genetically determined (Endler 1977, Lack *et al* 2015), the population of *T. lactitarse* is composed by females that behave as long-distance dispersers and it reinforces the hypothesis of the dependence of the populations living in TR on females constantly migrating from other sites. Additionally, large wings need more energy for their development and, in an environment with limiting resources, these structures are more susceptible to the FA caused by stress during their development (Leung & Forbes 1996). Although larger wings may be a feature that facilitated the occupation in TR by females, it possibly does not remain stable throughout the generations. The males born in TR have an inverse WL pattern in relation to females. Their higher WL reflects a higher body weight (Polidori *et al* 2013). Studies indicate that the increase in WL is positively related to the increase in the flying musculature (Kemp & Alcock 2008; Yao 2011). Although greater flight musculature results in higher energy expenditure, individuals with these characteristics present greater maneuverability and acceleration during their foraging (Marden 1989). In a study on a “cicada killer” wasp, greater competitive success was observed in territorial males with higher flying musculature (Coelho & Holliday 2001), and the same pattern was found for dragonflies (Marden 1989). Some studies show that *Trypoxyylon* males may exhibit territorial behavior to increase the chances of reproductive success (Alcock 1975; Buschini & Donatti 2012); therefore, a greater flight musculature may give them more success for intercepting the long-distance female since they can take off with greater speed (Byrne *et al* 1988). Thus, environments with low availability of females may have favored males with higher WL, since this feature seems to increase the success in interception of females for mating.

As expected, among the different habitat types evaluated, pastures were inadequate for the establishment of *T. lactitarse*. This demonstrates the need for reforestation to recover local populations from deforested areas. However, the different types of tree plantations presented a lower efficiency in the recovery of population patterns in relation to natural regeneration areas (secondary forest). The planted species used in the present study, especially *Tectona grandis*, probably did not favor the recovery of environmental conditions that could aid in the re-establishment of *T. lactitarse* population patterns. The success of secondary

forest was possibly due to its proximity to the primary forest (source of colonizing species). This may have facilitated the establishment of native species and consequently led to the development of more similar characteristics found in natural environments, such as food availability and adequate environmental conditions. However, the effectiveness of secondary forests from abandoned areas may fail in regions without the presence of nearby natural forests. This demonstrates that environmental recovery projects should be evaluated individually, taking into account the characteristics of each area to be recovered.

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