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Influence of forest cover and sex on wing size and shape of a spider-hunting wasp in the Brazilian Atlantic forest

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Abstract

1. Habitat loss and fragmentation are major drivers of biodiversity decline, affecting species persistence and morphological traits such as wing structure.
2. In insects, wing shape influences flight efficiency, foraging and dispersal capacity, making it a sensitive indicator of environmental pressure.
3. We investigated how landscape structure affects wing size and shape in the solitary wasp *Trypoxylon lactitarse* in the Brazilian Atlantic forest, using trap nests across gradients of forest cover, edge density, heterogeneity and connectivity.
4. Geometric morphometrics and statistical models were used to assess the effects of these landscape metrics on forewing size and shape.
5. *T. lactitarse* females exhibit longer and narrower wings in areas with higher forest cover, suggesting sex-specific morphological sensitivity linked to differing ecological roles, while female wing size and male morphology remain unaffected.
6. These results indicate that female wing shape reflects ecological pressures associated with landscape alteration and emphasizes the importance of preserving forest cover to maintain the functional integrity of neotropical wasp populations, with important implications for biodiversity conservation.

KEYWORDS
flight, geometric morphometrics, landscapes, phenotypic plasticity

INTRODUCTION

Habitat loss and fragmentation (hereafter habitat fragmentation) is the main cause of global biodiversity decline (Gray et al., 2018). In addition to threatening the existence of many species and ecosystems, these changes influence the rate of climate change, species distribution and a community's composition and dynamics (Laurance & Vasconcelos, 2009; Moura et al., 2012; Porensky & Young, 2013). Some studies indicate that habitat modification also leads to direct changes in the morphological traits of living beings (Yates & Andrew, 2011), which are crucial for the individual performance of each organism, such as the ability to utilize resources required for their reproduction and survival (Buchholz & Egerer, 2020).

In fragmented landscapes, species either migrate or adjust to the conditions through genetic adaptations or phenotypic plasticity (Vandewoestijne & Van Dyck, 2011). During embryonic development, organisms may encounter genetic or environmental disturbances that can result in phenotypic modifications (Nunes et al., 2015), although not all these phenotypic responses are adaptive (Via et al., 1995). Many studies have focused on understanding how insects respond to

different environmental conditions and resource availability through variation in their morphological traits (Gagic et al., 2015). For example, microclimate differences are key factors in generating morphological diversity in flying insects (Mena et al., 2020). Due to varying environmental conditions during nest construction, an insufficient supply of food resources may result in developmental stress in offspring, leading to morphological changes in individuals (Niemi & McDonald, 2004; Sanseverino & Nessimian, 2008; Yates & Andrew, 2011).

Pressure from habitat fragmentation can lead to different phenotypic expressions in animals, as observed by researchers who have recorded significant changes related to insect wing morphology (Brito et al., 2018; Gibbs & Van Dyck, 2010; Hirschfeld et al., 2021). These findings have raised concern among scientists, as wings play a critical role in ensuring the stability and manoeuvrability of flight, which are traits closely linked to individual fitness (Wootton, 1992; Wootton, 2002). Flight can significantly impact insects' range from foraging areas, as well as their ability to search for oviposition sites or mating partners, thereby influencing reproductive success (Berwaerts et al., 2002; Van Dyck & Matthysen, 1999).

Several studies have sought to understand how habitat fragmentation, landscape heterogeneity and varying environmental conditions may influence insect wing shape and size (Benítez et al., 2008; Mena et al., 2020; Outomuro et al., 2013). Previous work on these animals, such as by Merckx and Van Dyck (2006), observed that developing larvae of the butterfly species *Pararge aegeria* (Linnaeus, 1758) in agricultural landscapes had greater thoracic mass and wing loading than individuals in forested landscapes. Studies on *Euglossa* (Latreille, 1802) bees, collected at forest fragment edges and interiors, showed significant differences in wing symmetry, suggesting that wing shape alterations resulted from developmental instability in the larvae (Silva et al., 2009). Researchers noted that heterogeneous and unstable environments appear to favour individuals with longer wings, associated with greater flight aerodynamics, as these wings allow for greater speed and flight distance than shorter and wider wings (Berwaerts et al., 2002; Berwaerts & Van Dyck, 2004; Mena et al., 2020). Studies on *Bombus* (Latreille, 1802) and *Euglossini* (Latreille, 1802) bees found that land-use changes seemed to favour individuals with longer wings, suggesting that larger wings enable longer foraging trips in habitats where resources are scarce (Brito et al., 2021; Murúa et al., 2011).

To better understand this relationship, ecologists have been investigating how flight characteristics, in the context of spatial variation, may result from adaptations to landscape structure modifications (Hassall, 2015). However, most of these studies were conducted among different species from the same community, and only a few examined population-level variations within a single species (Hoffmann & Shirriffs, 2002; Loh & Bitner-Mathé, 2005). Furthermore, few investigations have focused on wasps (Brock et al., 2021; Santoni et al., 2023; Yüksel & Tüzün, 2011), which play an essential role in ecosystem functioning, as they contribute to the biological control of other species and pollinate many plant species. As a result, these processes are poorly understood (Brock et al., 2021).

Many species of wasps, both social and solitary, are impacted by the effects of ongoing environmental degradation. There is substantial evidence that populations of these insects are declining at alarming rates due to natural habitat modifications (Outhwaite et al., 2020). Thus, selecting a suitable model for study can be essential to understanding the whole process of environmental impact on species phenotypes and, consequently, on individual fitness. We selected *Trypoxylon lactitarse* Saussure, 1867 (Crabronidae) as a promising model for this investigation, as it is easy to capture, occurs in both conserved and degraded habitats (Araújo et al., 2018; Buschini et al., 2006), and its geographic distribution extends from southern Canada to southern Argentina (Coville, 1981). *Trypoxylon lactitarse* is a common solitary wasp that nests in pre-existing cavities and uses spiders as food for its offspring (Buschini et al., 2006). Although *T. lactitarse* is a habitat generalist species, its larvae are also under the effect of food availability and environmental stresses, such as the loss and fragmentation of habitat, which may be expressed by phenotypic changes in these new individuals (Buschini et al., 2010; Moura et al., 2019). Therefore, this species could serve as a good model for addressing both ecological and evolutionary questions, as changes in these individuals affect not only their current survival but also that of future generations.

This research addresses the following question: does landscape structure influence the size and shape of the wings of *T. lactitarse*? Our hypothesis is that such an influence exists, as previous studies indicate that forest cover (%), edge density (m/ha), heterogeneity and structural connectivity (%) influence developmental stress in insects, leading to alterations in wing morphology (Nunes et al., 2015; Via et al., 1995). Furthermore, it is known that wing dimensions and shape are fundamental for flight stability and efficiency, directly affecting foraging ability, mate search and, consequently, individual survival (Van Dyck & Matthysen, 1999; Wootton, 1992). Research on various hymenopteran and lepidopteran groups shows that populations in more fragmented landscapes or under intense edge effects tend to exhibit longer wings and greater morphological variability, possibly in response to unstable microclimates and limited resource availability (Mena et al., 2020; Merckx & Van Dyck, 2006; Silva et al., 2009). Considering that *T. lactitarse* occurs across a wide range of environments, from well-preserved areas to degraded landscapes, it is reasonable to assume that its wing morphology reflects these spatial and environmental pressures.

MATERIALS AND METHODS

Study area

This study was conducted using data collected from 2022 to 2023 in the Cantareira-Mantiqueira Corridor region, part of the Atlantic forest biome in the state of São Paulo, Brazil (Figure 1). The study area is part of the Long-Term Ecological Research of the Cantareira-Mantiqueira Corridor (LTER CCM or PELD CCM in Portuguese), which has been ongoing since 2014. Many studies have been conducted in this region to understand the effects of landscape structure on various dimensions, such as biodiversity, ecological functioning and ecosystem services.

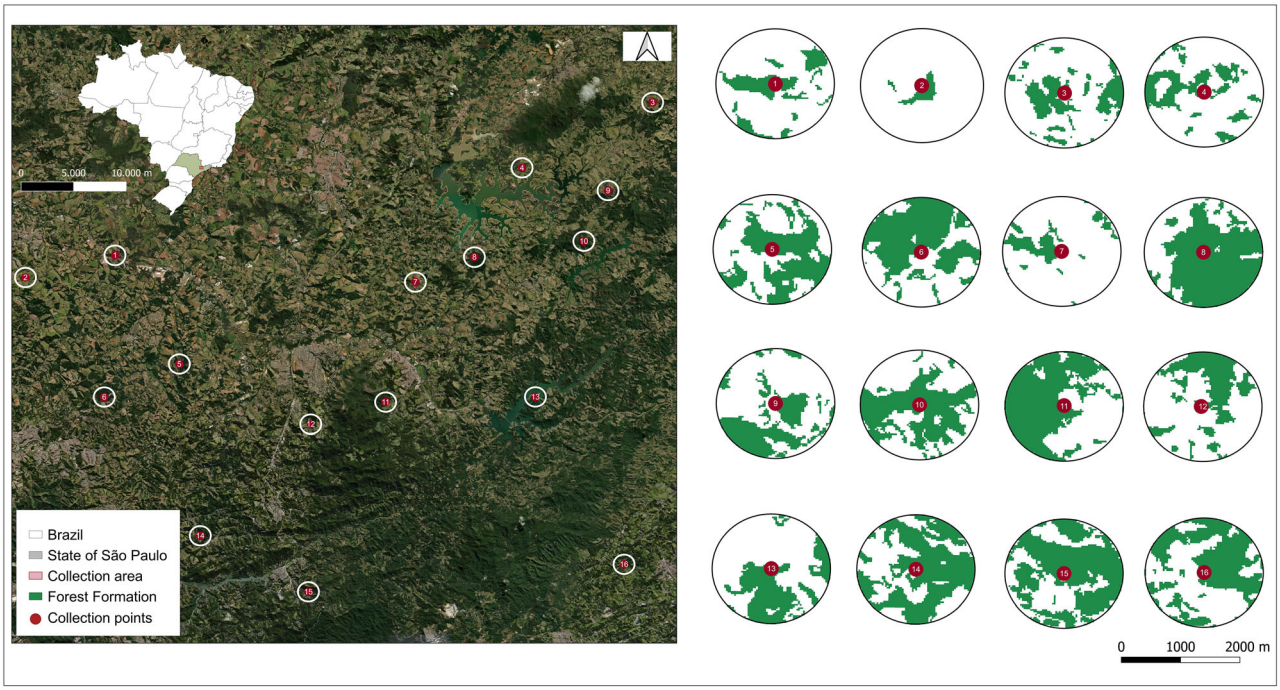

FIGURE 1 Sampling site locations (centre of each landscape—1 km radius buffer) along the Long-Term Ecological Research at the Corridor Cantareira-Mantiqueira (LTER CCM), Atlantic Forest, Brazil.

According to the Köppen climate classification, the region has a humid subtropical climate with an average minimum temperature of 8.6°C, an average maximum temperature of 29.5°C, and an average annual rainfall of around 1500 mm. The hottest and most humid months are from October to March, and January is the hottest month. The region has 10 conservation units, including state parks and protected environmental areas (Mazzei, 2007). The vegetation comprises High-Altitude Grasslands, Dense Ombrophilous Forest, Lower Montane Rainforest and Montane Rainforest.

Data collection

Trypoxylon lactitarse were collected using the trap-nest method, following the procedures described by Buschini et al. (2006), Buschini and Woiski (2008), and Nether et al. (2019). To increase the chances of successful nesting and capture, two types of traps were used. The first type consisted of black cardboard tubes, each 8 cm long and with a diameter between 0.6 and 0.8 cm, closed at one end. These tubes were grouped in sets of 25 and placed inside polyethylene terephthalate (PET) bottles (1 L). The second type used bamboo canes of varying lengths (from 8 to 20 cm) and cavity diameters (ranging from 0.6 to 1.3 cm), also sealed at one end, with 25 canes stored in each bottle. At each sampling point, positioned at the centre of each landscape, a station was set up with a wooden stake holding two PET bottles filled with cardboard traps and two with bamboo traps, totalling 100 potential nests per sampling point. Using both materials helped ensure a broader appeal to the wasps, as cardboard provides consistency for measuring morphological traits, while bamboo better mimics natural nesting conditions, offering a more realistic snapshot of their ecological preferences.

Each landscape was visited monthly to collect nests during the hottest and most humid period of the year, from August to May, between 2022 and 2023. The nests used by the species were removed from the field and replaced with another empty one of similar size. They were then taken to the laboratory, where they were kept at room temperature inside test tubes or PET bottles of appropriate diameters, sealed with cotton. Once the individuals emerged, they remained trapped inside these tubes, where they were collected. Each individual was euthanized with ethyl acetate, pinned and identified.

Subsequently, 314 *T. lactitarse* specimens (Figure 2a) from 16 landscapes were selected for morphometric analysis, of which 160 individuals were identified as females and 154 as males. The right forewings of these specimens were removed and placed on slides for microscopy. Once this step was completed, the wings were photographed under a Leica stereo microscope attached to a camera to study the existing venation patterns (Figure 2b).

The wing images were first converted into Thin Plate Spline (TPS) format using the software tpsUtil 1.60 (Rohlf, 2013). Next, using tpsDig 2.0 (Rohlf, 2015), we identified and digitized 11 anatomical landmarks (Figure 2b). These landmarks correspond to intersections of veins and other morphologically stable regions of the wing, which ensure consistent identification across individuals. We chose these specific landmark positions because they are widely recognized in geometric morphometrics for their biological relevance and homology, meaning they represent the same structures across all specimens

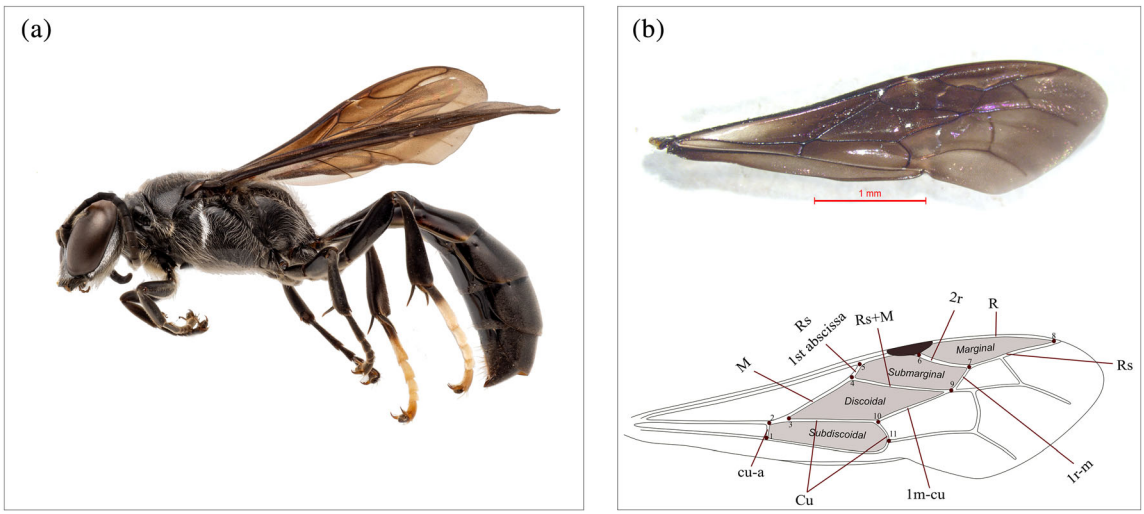

FIGURE 2 (a) Female *Trypoxylon lactitarse* (photograph by Prof. Dr. Eduardo A. B. Almeida). (b) Right forewing, showing anatomical landmarks (1–11) used for morphological analysis. Vein and cell nomenclature follow Bohart et al. (1976).

(Zelditch et al., 2012). By mapping their positions as Cartesian coordinates, both the size and the shape of the wings can be accurately captured.

The spatial arrangement of these landmarks allows for precise shape analysis, while their distribution also enables the calculation of centroid size, a commonly used proxy for overall wing size. As wing venation is closely tied to flight performance and developmental processes, variations in these geometric patterns can provide valuable insights into the effects of environmental or evolutionary pressures (Klingenberg, 2010).

Landscape analysis

Landscape metrics were calculated using land use classification maps provided by MapBiomas, a Brazilian collaboration initiative involving non-governmental organizations, universities and companies, which has provided spatial data covering the entire Brazilian territory from 1985 to the present (Souza et al., 2020). The land use data has a spatial resolution of 30 metres, with a mapping scale of 1:5000. For each of the 16 sampled landscapes, we defined a study area with a 1 km radius from the central point of each landscape. The map subsets were then extracted using the *sf* (Pebesma, 2018) and *raster* (Hijmans, 2023) packages in R software.

The choice of a 1 km radius to delineate the landscapes is justified by its ecological relevance for solitary Hymenoptera. This spatial scale is recognized in the literature as representative of the foraging and dispersal range of most of these insects, directly influencing resource availability and their movement within the environment (Montagnana et al., 2021).

To compute landscape metrics, we used the *landscapemetrics* package in R. This package enables both quantitative and qualitative landscape analysis based on categorical land cover classifications. The land use classification defined forest as Dense, Open and Mixed Ombrophilous Forest and Seasonal Forest Semi-Deciduous, Seasonal Deciduous Forest and Pioneer Arboreal Formation (Souza et al., 2020). As explanatory variables, we computed:

1. *Forest cover (%)*: Percentage of the landscape covered by forests. It is a crucial indicator of habitat availability and reflects the extent of native vegetation in the area, which is vital for forest-dependent species (Gardner et al., 2009; Lira et al., 2012).
2. *Structural connectivity (%)*: Degree of physical connection among forest fragments, showing the cohesion of forest vegetation in the landscape. This is fundamental for species movement and dispersal (Maximilian & Hesselbarth, 2023; Taylor et al., 1993).
3. *Edge density (m/ha)*: Measures the total length of edges in metres per hectare between forest and other land uses within 1-km landscapes. High values indicate greater fragmentation and the presence of transition zones, which can affect local fauna (Arroyo-Rodríguez et al., 2017; Razafindratsima et al., 2018).
4. *Landscape heterogeneity*: Expresses the diversity of land uses and covers in the landscape, considering both the variety of classes and their distribution. Higher values indicate a greater diversity of available habitats (Fahrig et al., 2011; Maximilian & Hesselbarth, 2023).

The analyses of explanatory variables revealed a wide variation in landscape metrics among the sampled areas (Table S1): forest cover ranged from 4.04% to 69.77% (mean = 39.28% ± 20.90), the structural connectivity varied from 93.37% to 97.76% (mean = 95.47% ± 1.69), edge density varied from 3291 to 32,851 m/ha (mean = 17,724.99 m/ha ± 7134.06), and the landscape heterogeneity index ranged from 0.82 to 1.58 (mean = 1.185 ± 0.23).

Morphometric analysis of wings

Since *T. lactitarse* males are smaller than females (Buschini, 2007), we chose to analyse them separately, thus also taking into account the

sex effect. To measure the wing size, we used the centroid size, which is essentially the square root of the sum of the squared distances from each anatomical landmark to the centre of the wing (Monteiro & Reis, 1999).

To analyse the wing shape, we applied a Procrustes Superimposition Analysis. We used this method to 'remove' differences caused by size, position and orientation of the wings, allowing us to focus solely on the true shape differences. Therefore, we can precisely compare the wing structures among individuals without size interfering (Adams et al., 2004). From this, we obtained coordinates that represent shape variation, which helps us analyse morphological differences between the wings.

Therefore, wing shape is defined as the geometric configuration of anatomical landmarks outlining the wing contour and veins, after removing the effects of size, position and rotation. Each shape is represented by coordinates in a multidimensional space (Langerhans, 2009; Langerhans & DeWitt, 2004; Rohlf, 2015), without an intrinsic scalar value. Values considered 'high' or 'low' refer to relative positions along the principal axis of shape variation; for instance, individuals at one extreme may have wings that are relatively longer and narrower, while those at the opposite extreme may have wings that are relatively shorter and wider, depending on the studied population and environmental gradient.

Importantly, there are no theoretical numerical limits for wing shape; the observed variation reflects the range of biologically viable and adaptive forms within the studied population (Langerhans, 2009; Langerhans & DeWitt, 2004).

Statistical analysis

To analyse wing shape, we based our analysis on coordinates obtained from a Procrustes analysis, which transforms the wing landmarks into a state of maximal superimposition for further comparison (Peres-Neto & Jackson, 2001). First, to identify which explanatory variable best explained the wing shape, we performed a multivariate analysis of variance (MANOVA), following the approach of Langerhans (2009). In this analysis, we used the scores from a Principal Component Analysis (PCA) as response variables, which reduced the dimensionality of the shape data derived from the Procrustes coordinates, using the first 12 principal components. This explained more than 80% of the variation. As explanatory variables, we included sex, wing size and landscape metrics. The MANOVA model was represented as:

$$\text{Wing shape}(\text{PC1} - \text{PC12}) \sim \text{Log}(\text{Centroid Size}) + \text{Forest Cover} + \text{Structural connectivity} + \text{Edge density} + \text{Landscape heterogeneity}.$$

The log-transformed centroid size was included as a covariate to account for allometric effects, allowing us to separate variation due to wing size from variation attributable to landscape metrics.

Second, to analyse the effect of the landscape on the wing shape, we used generalized linear mixed models (GLMMs), using a *Gaussian* error distribution, with an *identity* link function, using the *glmer* function from the *lme4* package (Bates et al., 2015). To better reproduce the wing shape as a response variable in the model, we used the method proposed by Langerhans and DeWitt (2004), which used the matrix of sums of squares and cross-products (SSCP) from the MANOVA analysis previously conducted. Considering the values, we derived canonical axes of shape variation associated with environmental predictors, meaning that we had a unique value of the shape of wings for each landscape (continuous variable). Finally, we used the landscape metrics of forest cover, structural connectivity, edge density and landscape heterogeneity as explanatory variables. To avoid potential collinearity among these metrics, we fitted a separate GLMM for each one. For example, the model assessing edge density was represented as:

$$\text{Wing shape} \sim \text{Edge Density} + (1 \mid \text{Landscape}).$$

Analyses were performed separately for males and females. The wing shape values used in the GLMM had been previously adjusted for allometric effects in the MANOVA.

Additionally, we performed a similar GLMM analysis to investigate the influence of landscape metrics on wing size. In this model, centroid size was the response variable, and the same landscape metrics were used as explanatory variables. The model structure followed the same logic in terms of error distribution and link function; however, the random effect was the landscape identifier to account for variation among landscapes.

Third, to visualize the wing shape changing among landscapes, we conducted a canonical variate analysis (CVA) using the Procrustes coordinates as response variables. To optimize group discrimination among landscapes, we transformed the explanatory continuous landscape metrics into categorical ecologically meaningful classes. Therefore, we classified forest cover in four categories: (1) less than 20% cover, (2) >20% to 40% cover, (3) >40% to 60% cover and (4) >60% to 80% cover. The structural connectivity was classified in three categories: (1) less than 94%, (2) >94% to 96% (3) >96% to 98%. Edge density was also classified into four categories: (1) less than 10,000 m/ha, (2) from 10,001 to 15,000 m/ha, (3) from 15,001 to 20,000 m/ha and (4) from 20,001 to 25,000 m/ha. Finally, landscape heterogeneity was classified into three categories: (1) <1.0, (2) >1.1 to 1.5, (3) >1.5 to 2. In some multivariable analyses, such as the CVA, the categorization of continuous variables into discrete data can improve group discrimination and thus strengthen our visualization of patterns, such as the wing shape between categories of landscapes (Khattree & Naik, 2000; Klingenberg, 2010).

Wing measurements (Centroid size, Procrustes analysis, PCA and CVA) were performed using MorphoJ version 1.06 (Klingenberg, 2008), while all other statistical analyses and modelling were conducted in R version 4.1.2 (R Core Team, 2021).

RESULTS

Influence on wing shape

The MANOVA indicated that both centroid size (Wilks' $\lambda = 0.23$, $F = 79.72$, $p < 0.01$) and sex of the individuals (Wilks' $\lambda = 0.52$, $F = 22.67$, $p < 0.01$) exerted highly significant effects on the wing shape of *T. lactitarse*. The landscape metrics also showed a significant effect (Wilks' $\lambda = 0.91$, $F = 2.21$, $p = 0.01$), although with a smaller explanatory magnitude, as reflected by the Wilks' λ value closer to 1. Additionally, we observed a significant interaction between sex and landscape (Wilks' $\lambda = 0.92$, $F = 1.09$, $p = 0.03$), suggesting that the influence of landscape characteristics on wing shape varies between males and females.

In the GLMMs, which used wing shape as the response variable, it was observed that among the four analysed landscape metrics, only forest cover (%) had a statistically significant effect on the wing shape of females (Estimate $= -8.54 \times 10^{-5}$; $p = 0.03$; Adjusted $R^2 = 0.19$). Despite its low magnitude, the coefficient aligned with the pattern can be seen in the graphical analysis (Figure 3), indicating a subtle but ecologically meaningful effect. For males, none of the tested environmental variables showed statistical significance (Table 1).

Visual analysis of wing shape (CVA)

CVA revealed visual patterns in wing proportions of specimens across different landscape categories. The first two canonical axes explained 83.7% of morphological variation in females and 79.5% in males (Figure 4). In *T. lactitarse* females, we observed a narrowing of the wings associated with an increase in forest cover. This result was mainly associated with the first canonical axis (60% of shape variation), which highlighted this narrowing along with elongation of marginal and submarginal cells, resulting from shortening of veins 2r, Rs + M, and 1r-m, and lengthening of veins R and Rs (Figure 4a,b).

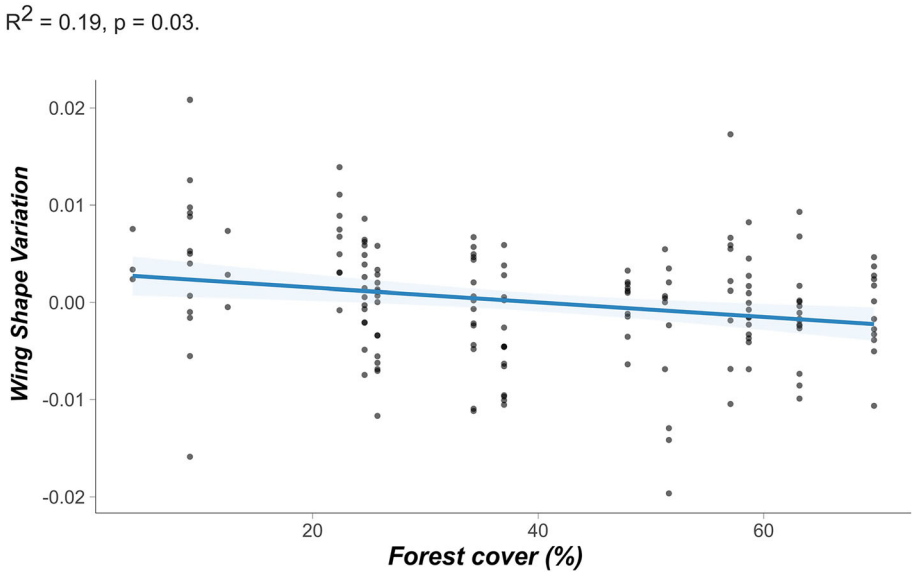

FIGURE 3 Linear regression showing the variation in wing shape of female *Trypoxylon lactitarse* based on forest cover in different landscapes.

TABLE 1 Fixed effects for the generalized linear mixed model (GLMM) calculated for the wing shape of male and female specimens of *Trypoxylon lactitarse* within Atlantic Forest, Brazil.

Male (♂)					Female (♀)			
Predictors	**Estimate**	**SD**	r^2	p	**Estimate**	**SD**	r^2	p^*
Forest cover	<0.0001	<0.0001	0.17	0.57	<0.0001	<0.0001	0.19	0.03
Landscape heterogeneity	0.0045	0.0045	0.17	0.36	0.0010	0.0037	0.20	0.78
Structural connectivity	−0.0009	0.0006	0.17	0.11	−0.0008	0.0005	0.20	0.10
Edge density	<0.0001	<0.0001	0.17	0.55	<0.0001	<0.0001	0.17	0.14

Note: GLMM models were run using landscape metrics and Centroid size as fixed effect predictors, while the Landscape ID was included as a random factor in the model.
*$p < 0.05$ is significant.

For males, there was a widening of wings relative to different forest cover categories (%), where the marginal cell was longer due to increased length of veins R and Rs, while the submarginal, discal and subdiscal cells were shorter and wider (CV1 axis, representing 48% of variation) (Figure 4c,d). Similar visual patterns for other landscape metrics can be found in Figures S1–S4.

Influence on wing size

None of the evaluated landscape metrics (forest cover, structural connectivity, edge density or landscape heterogeneity) had a statistically significant effect on wing size in *T. lactitarse* individuals, for either males or females ($p > 0.25$ for all variables) (Table 2). For males, estimated coefficients were low and accompanied by large standard errors, with *p*-values ranging from 0.42 (landscape heterogeneity) to 0.99 (edge density). Similarly, among females, the models did not detect significant associations, with *p*-values ranging from 0.25 (forest cover) to 0.78 (structural connectivity). These results suggest that the wing is minimally sensitive to the structural landscape variations considered in this study.

DISCUSSION

Our results indicate that forest cover (%) at a landscape level is a significant driver of wing shape variation in *T. lactitarse* females, despite having no evidence of the effects on males or wing size. These

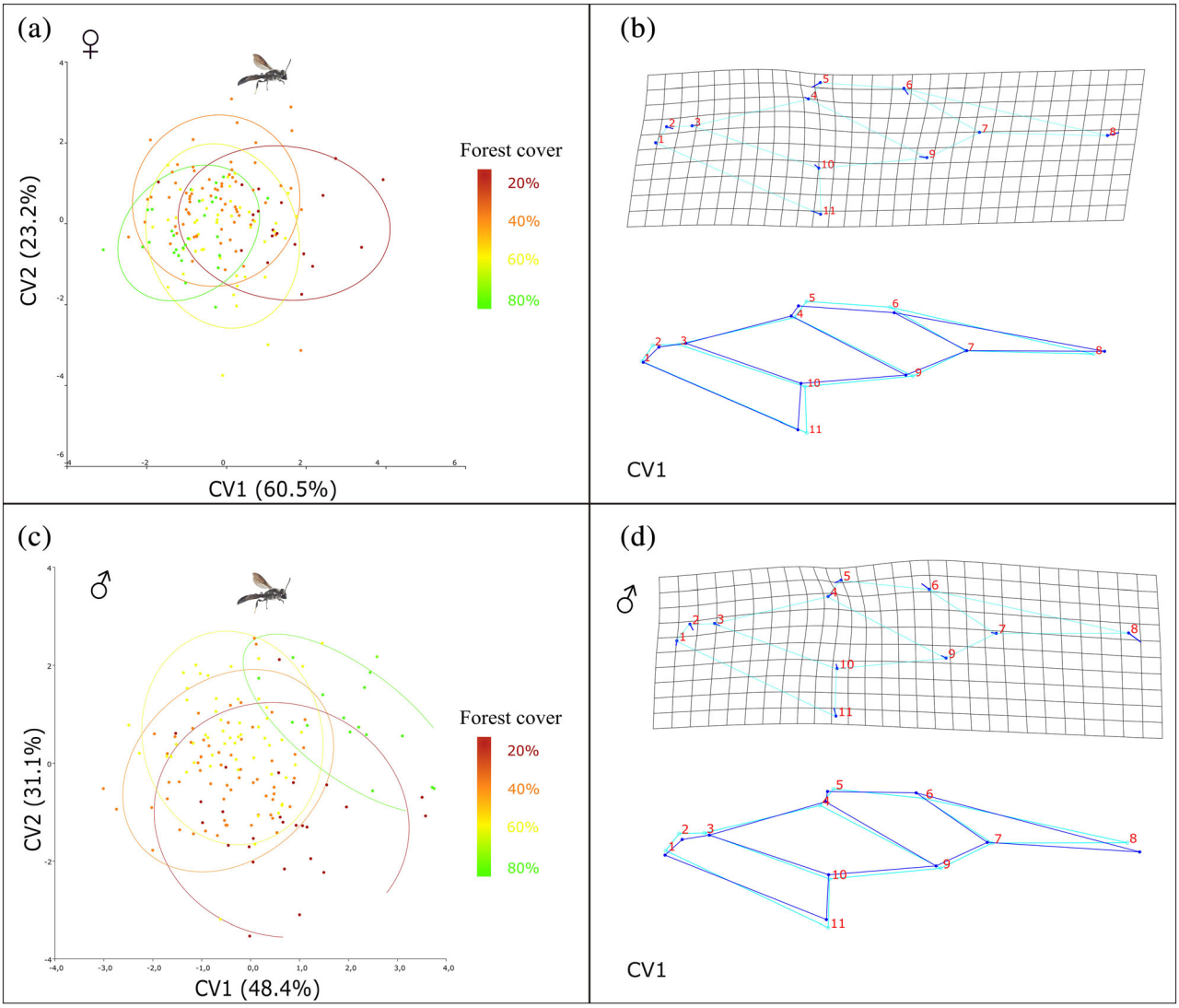

FIGURE 4 Deformation grids and wireframes illustrating wing-shape variation in female and male *Trypoxylon lactitarse* from the Brazilian Atlantic Forest in canonical space (CV1 and CV2). (a) Scatterplot of female wing shapes on canonical axes 1 and 2. (b) Deformation grid and wireframe showing deviations from the consensus shape along CV1 for females. (c) Scatterplot of male wing shapes on canonical axes 1 and 2. (d) Deformation grid and wireframe showing deviations from the consensus shape along CV1 for males. In the wireframes, light blue represents the consensus shape and dark blue highlights the greatest variation. Specimens are colour-coded by percentage of forest cover.

TABLE 2 Fixed effects for the generalized linear mixed model (GLMM) calculated for the wing size of male and female specimens of *Trypoxylon lactitarse*, Atlantic Forest, Brazil.

Male (♂)					Female (♀)			
Predictors	**Estimate**	**SD**	r^2	***p***	**Estimate**	**SD**	r^2	***p***
Forest cover	0.0001	0.0004	0.17	0.73	0.0004	0.0003	0.20	0.25
Landscape heterogeneity	0.0254	0.0315	0.18	0.42	0.0257	0.0294	0.21	0.38
Structural connectivity	−0.0007	0.0042	0.17	0.86	−0.0011	0.0041	0.20	0.78
Edge density	<0.0001	<0.0001	0.18	0.99	<0.0001	<0.0001	0.20	0.65

Note: The GLMM models were run using landscape metrics as fixed effect predictors, while the Landscape ID was included as a random factor in the model.

morphological variations may influence flight capacity and dispersal ability, which are key properties for population persistence in fragmented environments. This pattern supports our initial hypotheses and aligns with several studies showing that landscape simplification and habitat fragmentation can induce morphological changes in adult insects, with potential consequences for ecological performance and reproductive success (da Silva et al., 2018; Ferrari et al., 2024; Lima et al., 2014; Mena et al., 2020; Persson & Smith, 2011).

Insect wing shapes have been reported to be more sensitive to environmental pressures than wing size (Goldner & Holland, 2023; Hassall, 2015; Mena et al., 2020; Outomuro & Johansson, 2011). This occurs because shape is influenced by a broader range of functional and environmental factors, such as aerodynamics, flight efficiency, manoeuvrability, and response to environmental obstacles (Berwaerts & Van Dyck, 2004; Dudley, 2002). For example, studies with flies, such as *Polietina orbitalis*, have demonstrated marked variations in wing shape associated with environmental gradients, while wing size remained relatively constant (Alves et al., 2016). In the same way, this sensitivity in wing shape is also present in other insect groups, such as the wing morphology of the dragonfly *Calopteryx maculata*, which varies in response to forest fragmentation at regional scales of 1 to 5 km, which is mainly linked to forest edge density (Goldner & Holland, 2023). In these species of insects, there is a spatial autocorrelation in wing morphology based on linear traits, such as wing length and width, indicating that spatial processes have sufficient pressure to shape functional traits (Goldner & Holland, 2023). Thus, wing shape can represent a sensitive marker of ecological pressures in insects, revealing functional adaptations that are not captured by size alone.

Changes in wing shape have important functional implications. *Trypoxylon lactitarse* females exhibit longer and narrower wings in areas with higher forest cover, a morphology associated with greater aerodynamic efficiency, which reduces drag and increases lift, allowing more efficient flights during foraging and the exploration of nesting sites (Dudley, 2002). This wing configuration favours greater flight range without a proportional increase in energy expenditure (Berwaerts & Van Dyck, 2004; Norberg, 1990). In contrast, shorter and broader wings, which favour manoeuvrability and lift at low speeds during short flights in dense vegetation (Berwaerts et al., 2002; Berwaerts & Van Dyck, 2004), were observed in males of *T. lactitarse* in this study. Similar wing morphologies in *Bombus* bees have been linked to long-distance movement and territorial behaviour (Murúa et al., 2011), suggesting that sexual dimorphism in wing shape in *T. lactitarse* may reflect distinct phenotypic changes shaped by differing ecological pressures within the same landscape context.

Although both male and female *T. lactitarse* are exposed to the same environmental conditions, only females exhibited significant variation in wing shape. This difference suggests that distinct selective pressures act on each sex. As females are directly involved in nest construction and prey collection for their offspring (nesting cavities, building materials and spiders), changes in wing shape resulting in less elongated and broader wings in areas with lower forest cover may reduce flight efficiency. This reduction affects both flight speed and range during foraging, potentially compromising long-term population persistence (Buschini, 2007; Buschini et al., 2006; Camillo et al., 1994).

Wing shape is primarily determined during larval development, which depends on the amount of food provisioned (Helm et al., 2021). Consequently, cumulative effects of habitat loss and fragmentation may reduce population viability across generations, as offspring with lower flight efficiency may struggle to gather food and reproduce successfully (Niemi & McDonald, 2004; Sanseverino & Nessimian, 2008; Yates & Andrew, 2011).

Given the critical importance of food availability during the larval development of *T. lactitarse* females, understanding their ability to collect trophic resources may be a valuable tool for predicting how this species will respond to environmental disturbances. Prey selection by *T. lactitarse* is flexible and adaptive, varying according to regional and seasonal spider availability (Buschini et al., 2008; Genaro & Alayón, 1994; Rehnberg, 1987). The species learns to hunt individually and specializes according to the local prey community (Moura et al., 2019), reinforcing its behavioural plasticity as a population, but their high sensitivity is at an individual level (Buschini et al., 2010; Camillo et al., 1994). As individual females may learn to collect only a limited range of spider species, highly disturbed landscapes could lead to undercollection of prey for their offspring, ultimately reducing overall population persistence.

As males do not participate in prey collection, their wing shape tends to be less influenced by environmental variation but may be more related to sexual selection, such as nest guarding and mating

(Brockmann & Grafen, 1989; Buschini, 2007). This pattern aligns with studies in other hymenopterans, in which wing morphology results from the interaction between ecological and sexual forces. For example, in *Tachysphex* wasps, Pretorius (2005) found significant sexual dimorphism in wing shape, with male wings displaying greater morphological variation, likely related to reproductive behaviours such as locating mates. Similarly, Perrard et al. (2012) showed that in social wasps of the genus *Vespa*, queens and workers, although both are female, exhibited distinct wing shapes not entirely explained by body size. This suggests that specific functional roles, such as dispersal in queens and foraging in workers, can also shape divergent morphologies, reinforcing the influence of ecological demands on wing design.

Sex-specific morphological responses have also been documented in other insect orders. For instance, in *Heliconius charithonia* (Lepidoptera), ecological and behavioural differences between males and females lead to wing dimorphism and distinct responses to environmental variation, with females showing traits linked to dispersal and males to reproductive behaviours (Ramos-Pérez et al., 2020). Similarly, studies on dragonflies such as *C. maculata* indicate that male wing morphology is shaped more by sexual selection for territorial displays and combat, while female wing shape responds more to environmental factors (Johansson et al., 2009). In birds, research has shown that male wing morphology often reflects reproductive strategies such as acrobatic flight during courtship displays, whereas female wing morphology is more optimized for efficient foraging flight (Stiles et al., 2005).

FINAL CONSIDERATIONS

Based on our findings, sexual dimorphism in *T. lactitarse* is a reflex of wing morphology responses to environmental changes. Our results highlight the importance of conserving and restoring forest cover at a landscape scale, as fragmentation and the loss of suitable habitat primarily threaten females. In haplodiploid species, such as *T. lactitarse*, females are solely responsible for nest construction and provisioning offspring, making them the key contributors to reproductive success. Therefore, this study contributes to our understanding of morphological changes in individuals due to regional pressures and highlights the importance of preserving phenotypic diversity to ensure the functional integrity of *T. lactitarse* populations, thereby helping to mitigate the ecological impacts of habitat fragmentation.

AUTHOR CONTRIBUTIONS

Alexsandra de Lima Klates: Conceptualization; investigation; writing – original draft; methodology; writing – review and editing; formal analysis; software; data curation; validation; visualization. **Jean Pablo Alves de Deus:** Methodology; formal analysis; data curation; writing – original draft; writing – review and editing; conceptualization; validation; visualization. **Milton Cezar Ribeiro:** Validation; visualization; resources; writing – review and editing; supervision. **Maria Luisa Tunes Buschini:** Project administration; supervision; resources; validation; visualization; writing – review and editing; writing – original draft.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15705936. For further details, see (Lima & de Deus, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Landscape metrics for the 16 landscapes where *T. lactitarse* was collected, Atlantic Forest, Brazil.

Figure S1. Scatter plots are generated from principal component analysis and canonical variables according to landscape metrics. Dispersion of male and female *T. lactitarse* in relation to canonical variables CV1 and CV2, shown on a Cartesian plane according to the ID.

Figure S2. Scatter plots are generated from principal component analysis and canonical variables according to landscape metrics. Dispersion of male and female *T. lactitarse* in relation to canonical variables CV1 and CV2, shown on a Cartesian plane according to the Edge of the Landscape.

Figure S3. Scatter plots are generated from principal component analysis and canonical variables according to landscape metrics. Dispersion of male and female *T. lactitarse* in relation to canonical variables CV1 and CV2, shown on a Cartesian plane according to the Landscape Heterogeneity (Shdi) of the Landscape.

Figure S4. Scatter plots are generated from principal component analysis and canonical variables according to landscape metrics. Dispersion of male and female *T. lactitarse* in relation to canonical variables CV1 and CV2, shown on a Cartesian plane according to the Forest Connectivity of the Landscape.

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