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EFFECT OF HERBIVORY ON FUNCTIONAL TRAITS OF PIPER SP. AT THE EXPERIMENTAL CENTER FOR AMAZONIAN RESEARCH AND PRODUCTION CEIPA-UEA, NAPO PROVINCE, ECUADOR

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ABSTRACT

Herbivory is a key ecological interaction in tropical ecosystems, yet its effects on the reproductive functional traits of *Piper* sp. across contrasting habitat types remain poorly understood. Twenty *Piper* sp. individuals were sampled across a riparian habitat and a cacao agroforestry margin at CEIPA-UEA, Napo Province, Ecuador. Foliar damage was classified using the Dirzo and Domínguez (1995) herbivory index. Inflorescence and infructescence number and length were recorded and analysed using mixed linear and generalized linear mixed models. All individuals showed foliar damage, with Category 1 (1–6% removal) most frequent at both sites. No significant difference in mean herbivory index was detected between zones ($P > 0.05$), nor was herbivory significantly related to any reproductive trait. Plant height and reproductive maturity were significant predictors of inflorescence length ($P < 0.001$). Reproductive functional traits in *Piper* sp. were driven primarily by plant ontogeny rather than herbivore pressure. The uniformly low foliar damage across both habitats suggests effective chemical defences, likely enhanced by light availability in the riparian zone. These findings contribute baseline evidence for plant–herbivore dynamics in managed and natural Amazonian landscapes.

KEYWORDS: Interaction; Functional Trait; Foliar Damage; Inflorescence; Infructescence.

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1. INTRODUCTION

Herbivory is a fundamental ecological interaction that plays a central role in structuring terrestrial ecosystems. Herbivorous organisms occupy a key position in food webs and strongly influence plant population dynamics, community composition, and ecosystem functioning (Adey, 2024). Through the consumption of plant tissues, herbivores impose selective pressures that shape plant morphology, physiology, and life-history strategies. Consequently, herbivory is recognised as one of the most important biotic forces driving plant evolution and ecological interactions.

In tropical ecosystems, herbivory tends to be particularly intense due to the high diversity and abundance of herbivorous organisms. Vegetation in tropical regions is exposed to a wide variety of folivores, which can substantially increase the level of foliar damage experienced by plants (Vega Rovira et al., 2020). This high herbivore pressure can significantly affect plant growth, survival, and reproductive success. Herbivores often select plants based on their nutritional quality, defensive traits, and environmental conditions. As a result, plants have evolved a variety of defensive strategies to cope with herbivore attack, including the production of specialized secondary metabolites that deter herbivores or attract beneficial organisms such as predators and parasitoids (Lokare et al., 2023). Understanding the extent of herbivore damage and the mechanisms by which plants respond to it is therefore essential for evaluating plant health, growth, and population dynamics (Adedayo et al., 2025).

The expression of plant traits is influenced by multiple factors, including ontogenetic development, phylogenetic constraints, physiological processes, and environmental conditions (Barton, 2024). Herbivory interacts with these factors by modifying plant growth and morphology through the selective consumption of different plant organs. Primary consumers can therefore generate selective pressures that contribute to variation in plant traits. In this context, the analysis of leaf traits and herbivore foraging patterns among functional groups is crucial for understanding plant–herbivore interactions and their role in shaping ecosystem processes (Lebbink et al., 2023).

In the Ecuadorian Amazon, environmental changes and alterations in climatic factors have been observed in recent decades, with potential negative consequences for biodiversity and ecosystem functioning (Álvarez-Lozano et al., 2023). These tropical forests harbor a high diversity of plant species, including members of the family Piperaceae, which belongs to the class Magnoliopsida and is widely distributed in lowland tropical forests and rainforests worldwide (Yuliana, 2023). The genus *Piper* is one of the most diverse genera within this family, comprising approximately 2,600 species (Sen & Rengaian, 2022). In Ecuador alone, 157 native species and 61 endemic species have been documented (León-Yánez et al., 2019; Vidari, 2022). Species of *Piper* are commonly found in humid environments and are frequently associated with riparian habitats, where high soil moisture and favorable microclimatic conditions support diverse plant and animal communities. The structural characteristics of riparian ecosystems often create a variety of microhabitats that can influence the distribution and activity of herbivorous organisms (Philbin et al., 2022).

Morphologically, species of the genus *Piper* are typically shrubs or climbing plants, often aromatic, and occasionally herbs or small trees. They possess simple alternate leaves and characteristic spicate inflorescences that are usually positioned opposite the leaves, while the flowers lack a perianth (Pugalenthi et al., 2025). Flowering in many *Piper* species generally occurs annually, whereas fruiting may occur throughout the year due to species-specific phenological patterns (Valentin-Silva, 2023). As members of an early-diverging lineage of angiosperms, Piperaceae species possess distinctive evolutionary and ecological characteristics that allow them to occupy specialized ecological niches and exhibit resilience to environmental disturbances (Sen & Rengaian, 2022).

Despite the ecological importance of herbivory in shaping plant performance and community dynamics in tropical ecosystems, the effects of herbivore damage on reproductive traits of plants remain insufficiently understood, particularly in species-rich genera such as *Piper* (Grele et al., 2024). Relatively little is known about how herbivore damage affects the reproductive traits of *Piper* species in different habitat types within the Ecuadorian Amazon. In particular, comparisons between natural riparian habitats and agroforestry systems remain scarce, even though these environments may differ considerably in terms of microclimate, light availability, and herbivore communities. Most studies examining plant-herbivore interactions in tropical forests have focused primarily on patterns of leaf damage or chemical defense mechanisms, while comparatively fewer investigations have explored how herbivory may influence reproductive structures such as inflorescences and infructescences. Furthermore, little attention has been given to how these relationships vary across contrasting habitat types, such as natural riparian environments and managed agroforestry systems

Therefore, this study contributes new insights by examining the relationship between foliar herbivory and reproductive traits of *Piper* sp. across two contrasting environments-a riparian habitat and the margins of a cacao agroforestry system, within the Ecuadorian Amazon. By integrating measurements of herbivory intensity with reproductive trait data, this research provides empirical evidence on whether herbivore damage influences reproductive investment in *Piper* species under different environmental conditions. To address these gaps, this study was guided by the following research questions:

1. Does the intensity of foliar damage caused by herbivory differ significantly between the riparian habitat and the margins of the cacao agroforestry system at CEIPA-UEA?
2. Is there a significant relationship between the herbivory index and the number and length of inflorescences and infructescences in *Piper* sp.?
3. Does plant height mediate the expression of reproductive functional traits (inflorescence and infructescence length) differently across contrasting habitat types in *Piper* sp.?

Thus, this study aimed to evaluate foliar damage caused by herbivory in *Piper* sp. by comparing herbivory categories between riparian habitats and the edges of a cacao plantation located at the Amazonian Research and Production Experimental Center (CEIPA) of the Amazonian State University in Ecuador. In addition, the study assessed whether herbivory influences reproductive functional traits of *Piper* sp., specifically the number and average length of inflorescences and infructescences in the studied environments.

2. LITERATURE REVIEW

2.1. Herbivory as a Structuring Force in Tropical Ecosystems

Herbivory is one of the most widespread forms of biotrophic interrelation organizing the terrestrial ecosystem, defining the constitution of plant communities, eliciting evolutionary novelty, and facilitating the energy and matter transfer across trophic pyramids (Pringle et al., 2023; Zeng, 2024). These processes are unusually strong in tropical areas. The latitudinal gradients in comparative analysis have established a consistent finding that the phytochemical features and frequency of herbivore predation are always greater in tropical communities than in subtropical forests or sub alpine forests, which is explained by the fact that herbivorous organisms are richer and more specialized in the tropics (Sun et al., 2024). It is estimated that tropical leaves lose an estimated 11% of their area annually to herbivores, which is significantly greater than in temperate systems. Most of that loss is done during the expansion phase of the leaf, when the tissues are nutritionally rich but are structurally vulnerable (Balaji & Jambagi, 2025; Sun et al., 2024). It is a basic ecological background where plant-herbivore interactions of Amazonian species like Piper are to be seen.

2.2. Plant Functional Traits and Their Relationship with Herbivory

The connection between plant functional trait and herbivory has had a fair share of scholarly attention in recent years, although the predictability of individual leaf characteristic is still debated. Multi-species designed in tropical montane rainforests established that individual level variation in species as opposed to central values of species-level species traits predicted most of a variability in herbivory, and hypothesized that environmental conditions and food web interactions are potentially as important as intrinsic chemical or structural properties of leaves alone in regulating herbivore damage (Schön et al., 2024). This result contradicts previous hypotheses that the economic spectrum properties of leaves including specific leaf area or nitrogen content can be effectively used to predict the rate of herbivory, and suggests that context-dependency is an inherent aspect of the plant-herbivore system.

Complementary work has also determined clearly functional syndromes in the tropical woody species, classifying them into low nutritional quality, defensive resistance, and tolerance strategies with plants under the tolerance syndrome presenting the greatest extent of observable foliar damage nearly 35-55% more in comparison to their chemically-defended or nutritionally poor counterparts (Ruiz-Guerra et al., 2021). Combined with the above research, these studies highlight the intricacy of the trait-mediated herbivory and clarify that the extent of damage cannot be explained by one plant feature alone.

2.3. Ecology and Chemical Defense Mechanisms of Piper

The genus Piper holds a particularly pedagogical place within this larger context. This was shown by a large-scale transplant experiment that cut across five neotropical sites revealing that intraspecific and interspecific diversity in Piper played significant moderating roles in patterns of herbivory, herbivorous insect richness and plant mortality, as well as water availability which acted as a moderating factor (Grele et al., 2024). Most importantly the decreases of intraspecific diversity caused quantifiable effects of herbivory equal in extent to the loss of interspecific diversity, demonstrating the significance in ecological context of within species variability in controlling interactions among plants and herbivores (Wetzel et al., 2023). The results can especially be applied in the research carried out in disturbed or agroforestry nearby areas where the population structure and the plant diversity can significantly vary compared to the natural reference communities.

Chemical ecology of species of the genus Piper also supports the use of the genus as a model to study plant defense. The Piper species produce a unique reproductive stage of secondary metabolites piperamides, terpenes, phenylpropanoids, and lignoids that act as herbivore deterrent and pollinator attractants at the same time (Brito Machado et al., 2021). Notably, profiles of secondary metabolites change throughout ontogenetic stages with seedlings and young plants generating chemically different profiles to adult conspecifics and may change herbivorous pressure at various life stages. This chemical defense plasticity in developmental trajectory could be an explanation in part why experiments of low foliar damage in Piper populations at least in adults are not rare even in herbivore-prone habitats.

2.4. Light Availability, Secondary Metabolites, and Habitat-Mediated Defense

Plant secondary metabolites production and accumulation is not only set by the biotic pressure but highly regulated by the light environment. Solar radiation has come to be known as a significant controller of secondary metabolite biosynthesis, and the stimulators of an increase in phenylpropanoid, flavonoid, and terpenoid biosynthetic pathways under UV-B and UV-A photoreceptor-mediated signaling pathways have been well-characterized (Wu et al., 2025). This practically implies that plants growing in more open and high-irradiance environments, such as the riparian margins and forest edges, may have more chemical defenses as compared to conspecific individuals growing in the dense shade of controlled systems in such as agroforestry like cacao.

This variation in chemical defense capacity mediated by light can be used to explain the hypothesis that the prevalence of herbivory can vary in sun-exposed and shaded microhabitats, although the same fauna of herbivores is involved, a hypothesis that has been confirmed empirically in related tropical species (Assunção et al., 2023). Divekar et al. (2022) further determined that plant secondary metabolites simultaneously act at various tropic levels by both deterring, through toxicity, and antifeedant activity, and assembling natural enemies by releasing herbivore-noted plant volatiles signaling to natural enemies that the plant is providing appropriate food.

2.5. Herbivory, Reproductive Traits, and Fitness Consequences

The impacts of the herbivory on plant investment in reproductive functions and the show of functional traits describing the attributes of reproduction has emerged as a more booming field of study. A study on a neotropical deciduous tree (Casearia nitida) showed that foliar damage accumulated through one season into the next session significantly reduced the number of inflorescent, flower number, and infructescence production of the next reproduction cycle, and, at the same time, foliar damage during the flowering season became more pronounced a feedback response that has potentially exponential implications of reproduction success (Quiroz-Pacheco et al., 2020). Interestingly, the timing as well as the severity of herbivore damage to plants was not only differentially related to the reproductive results but also the snapshot estimates of herbivory foliar damage may be inadequate to estimate the overall reproductive costs of herbivory on perennial plants.

On the landscape level, Schroeder et al. (2024) showed that sample changes in floral display mediation can occur by herbivores, such as the decrease in the count of flowers, which can be regarded as an indirect route through which land use repression may repress the reproduction of wild plants notwithstanding the direct devastation of the habitat. All these results result in the conclusion that the connection between herbivory and reproductive functional characteristics is not a proportional relationship that can be detected in a cross-sectional survey, but an indirect, time-lagged, and context-dependent relationship.

Overall, some major insights can be drawn about studying Piper species in Amazonian habitats in this literature. Herbivory in tropical systems is dependent on interaction between the intrinsic plant chemistry and ontogenetic stage, light availability, habitat structure and herbivore community structure, none of which act independently. The chemical complexity of Piper species, such as their ability to generate bioactive volatiles in response to reproduction, renders the herbivore insects with a considerable degree of resistance to the differing environments, perhaps suppressing the ability to detect damage differences between the differing environments. Moreover, the dissociation of foliar injury with the expression of reproductive traits seen in short-term experiments is consistent with general evidence of resource reallocation and compensatory adaptation to moderate levels of herbivory among plants.

3. METHODOLOGY

3.1. Study Space

The Amazonian Research and Production Experimental Centre (CEIPA) is located at kilometre 44 of the Puyo-Tena road within the Carlos Julio Arosemena Tola canton, Napo province, situated next to the Santa Clara canton of the Pastaza province in the Ecuadorian Amazon. The average annual temperature is between 25 and 30 °C, and the average annual rainfall is 2939 mm. Two areas were selected for sampling within the study site. Zone 1 is located at UTM coordinates 18M 178536W 9863118S near the bank of a small tributary of the Piatua River, located on the provincial boundary between the provinces of Pastaza and Napo, that connects the foothills of the eastern mountain range with the central Amazon. Zone 2 is located at UTM coordinates 18M 178534W 9863019S, where a technical program of cocoa cultivation treated.with organic fertilisers is located.

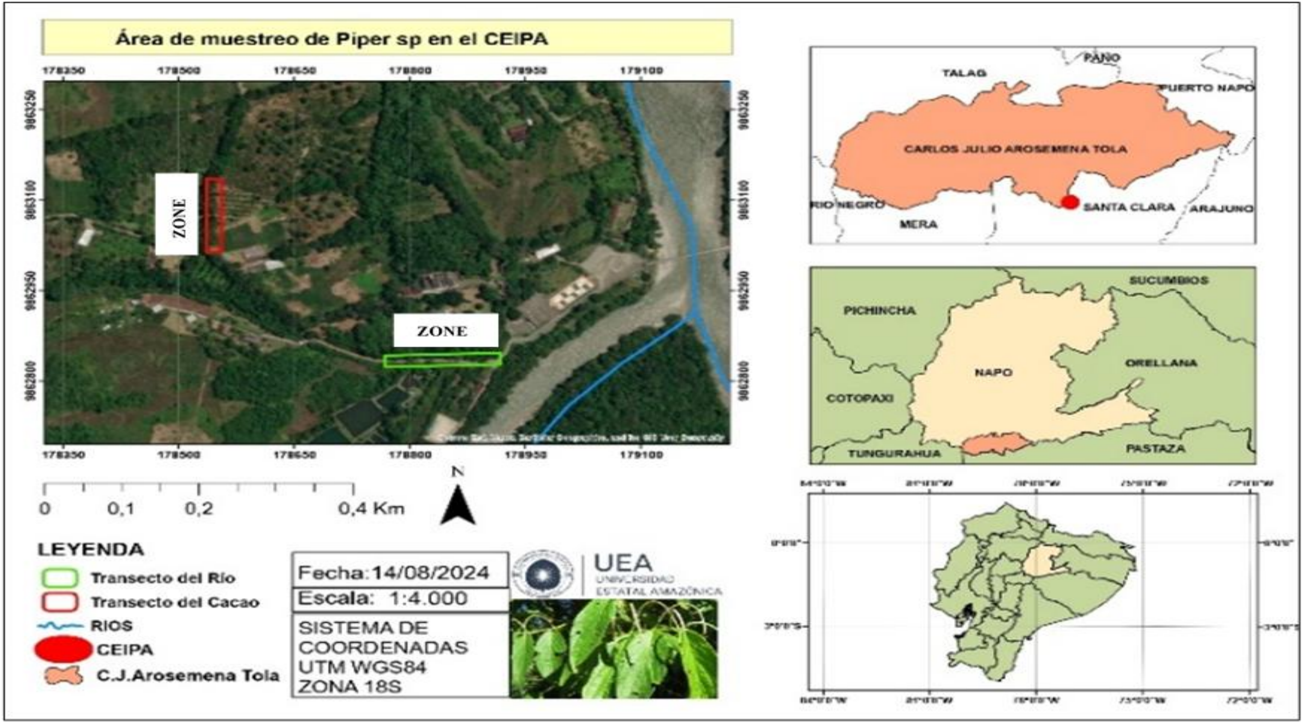

Figure 1: Map of the study area. The sampling zones in the CEIPA-UEA are shown in colour. The green rectangle is zone 1 (riparian habitat) and the red rectangle is zone 2 (cacao cultivation limits).

Figure 1 shows the CEIPA covers an area of 2848.20 ha of piedmont evergreen forest, located at an altitude of 400-2000 m above sea level, with a canopy that reaches 15 to 35 m in height.

3.2. Sample Collection

A path of approximately 50 m was marked out in each zone (1 and 2), and 10 Piper sp. individuals with a minimum height of 1.50 m were randomly selected, for a total of 20 individuals sampled across both sites, a path of approximately 50 m was marked out in each zone (1 and 2), and 10 Piper sp. individuals with a minimum height of 1.50 m were randomly selected, for a total of 20 individuals sampled between the two sites. Subsequently, the height of each plant was measured, and the number of inflorescences and infructescences present on each individual was recorded. Their length was measured, and the maturity stage of the flowers was considered according to their color: white to green for immature and brown to black for mature stages. Next, 20 leaves were randomly selected from each plant, taking into account the apical, middle, and lower zones of each individual. These were labelled and subsequently analysed for herbivory damage (Dirzo and Domínguez, 1995).

3.3. Index of Herbivory

To assess the intensity of foliar damage, the herbivory index proposed by Dirzo and Domínguez (1995) was used. In Figure 2, the selected leaves were classified in situ into six categories, taking into account the percentage of the leaf consumed by the herbivores. Category 0: absence of herbivore (0%), Category 1: 1-6% leaf removal, Category 2: 7-12%, Category 3: 13-25%, Category 4: 26-50%, Category 5: 51-100%.

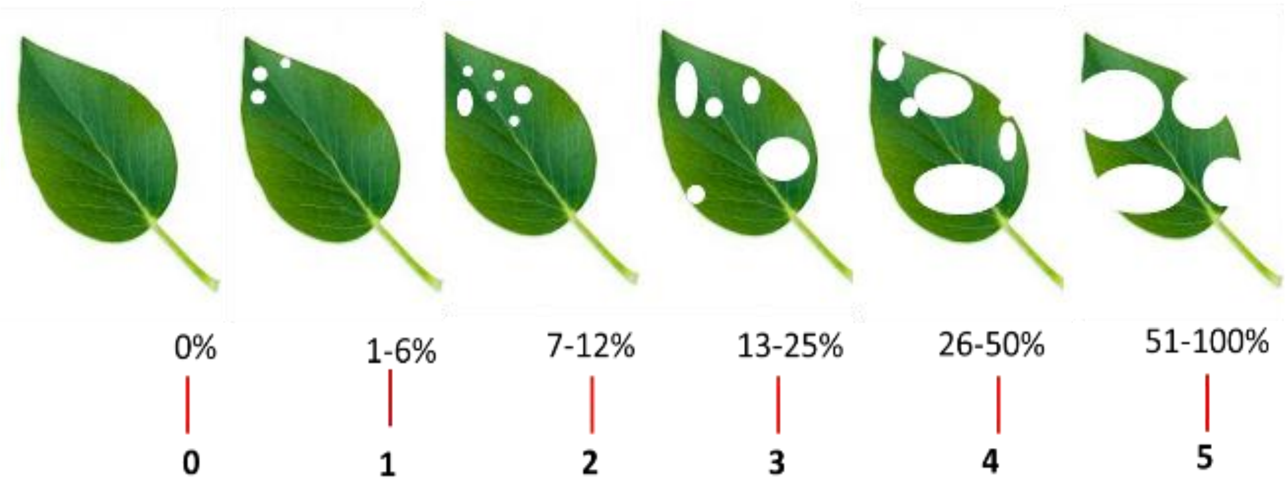

Figure 2: Category of damage caused by herbivory. Source: (Dirzo & Domínguez, 1995)

After the classification of the leaves, the herbivory index was calculated, which is the sum of the ratio between the leaves of each individual in each category over the total number of leaves analysed. Equation 1 shows that the index ranges from 0 when the leaf shows no signs of herbivory, while values up to 5 show that the leaf has more than 51% of its leaf area consumed.

$$\mathbf{IH} = \sum_{i=0}^{5}(X_i\, n_i)/\, N \qquad (1)$$

Where,

$X_i\, n_i$Number of leaves with damage in category i

N= total number of leaves

3.4. Data Analysis

To study functional traits, the length of the inflorescences and infructescences of selected Piper sp. individuals was considered based on the explanatory variable: study zones 1 and 2 (river and cacao, respectively). The analysis was performed using a mixed linear model, considering zones 1 and 2 as a fixed factor and the plants as a random factor. Additionally, the effect of plant height and the length of the inflorescences and infructescences, as well as their possible interactions, was analyzed. Adjusted means with standard errors were also obtained for each explanatory variable. Model validation was performed using a graphical analysis of the residuals.

Regarding the herbivory index analysis, the likelihood ratio test (the test of homogeneity of discrete distributions) was used to compare the foliar damage categories among the studied areas. Additionally, the proportion of leaves exhibiting foliar damage (categories 1–5 versus category 0) for each individual was compared between areas using a generalized linear mixed model with a binomial distribution, with the group (area) as a fixed factor and the individual plant as a random factor. This approach allowed comparison of mean herbivory probability between the two sites while accounting for the repeated-measures structure of the leaf-level data. Statistical analyses were performed using SAS v9.4 software (SAS Institute Inc., Cary, NC, USA). Statistical decisions were made using a significance level of 0.05.

4. RESULTS

4.1. Functional Traits Of Piper Sp.

A total of 433 inflorescences and 274 fruits were recorded in zone 1 (river) and 352 inflorescences and 39 fruits in zone 2 (cacao). When comparing the length of the flowers (mm) in both studied zones, no significant differences were found (P >0.05; F= 0.00), as well as in the length of the fruits (P >0.05; F= 0.62) (Figure 3). However, the height of the plants, the degree of maturation of the inflorescences and the relationship between both variables did show statistically significant differences (Table 1).

Table 1: Results of the fixed effects model related to inflorescence length, infructescence length, and functional trait variables in the river and cacao zones. * variables with statistical significance (P <0.05)

Variable	Num DF	Den DF	F Value	P Value	
	Inflorescence length				
Group (zone)	1	11	0.19	0.675	
Plant height (cm)	1	769	8.34	0.004	*
Degree of ripeness	1	769	29.82	<.001	*
Height*Degree	1	769	17.05	<.001	*
	Infructescence length				
Group (zone)	1	5	4.08	0.099	
Plant height (cm)	1	304	0.42	0.519	
Height* Zone	1	304	3.63	0.058	

*H.H. denotes the estimated regression coefficient (slope) for plant height from the linear mixed model

Therefore, the length of the flower is greater as the height of the plant increases. This effect is greater in flowers at an advanced reproductive stage (H.H. = 10.99) than in flowers with a lower degree of maturation (H.H. = 4.45). However, when analysing the effect of fruit length, only one interaction between height and the two study areas is detected, although this is not statistically significant (P = 0.058) (Table 1). Therefore, in zone 1 (river), the length of the fruit is greater as the altitude increases (H.H. = 18.63), whereas in zone 2 (cocoa), the length of the fruit decreases with the height of the plant (H.H. = -37.69).

The adjusted means for flower length indicated that plants from zone 2 (cacao) obtained higher scores (M=60.58, SE=10.28) than plants from zone 1 (river) (M=60.26, SE=9.62), as well as for fruit length, plants from zone 2 obtained the highest adjusted means (M=120.72, SE=13.15) than plants from zone 1 (M=112.21, SE=9.73).

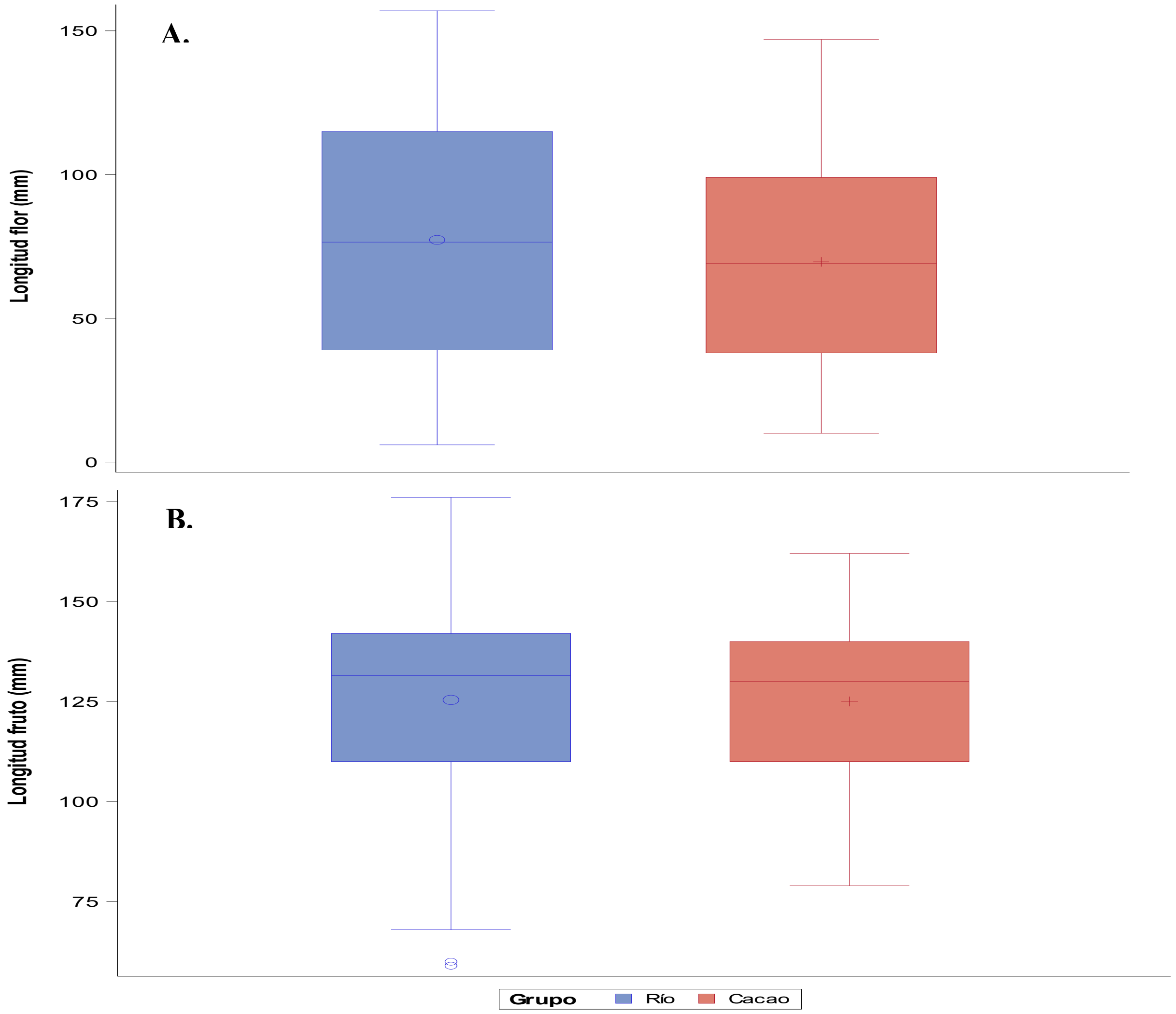

Figure 3: Box plots comparing the length of flowers (A) and fruits (B) in the two study areas.

4.2 Model Validation: Effect Of Flower And Fruit Length In The Studied Areas

The scatter plot for the analysis of the effect of flower length is not completely random. Two main groups can be observed, one around a linear predictor of 30 to 50 and another of 80 to 110. Furthermore, the variance of the residuals appears to be greater in the second group compared to the first (Figure 4A). This lack of uniform dispersion could suggest a heteroscedasticity problem, indicating that the variance of the model errors is not constant. Regarding the residual histogram, it can be observed that they fit the superimposed normal distribution curve well, and the distribution is relatively symmetrical (Figure 4B).

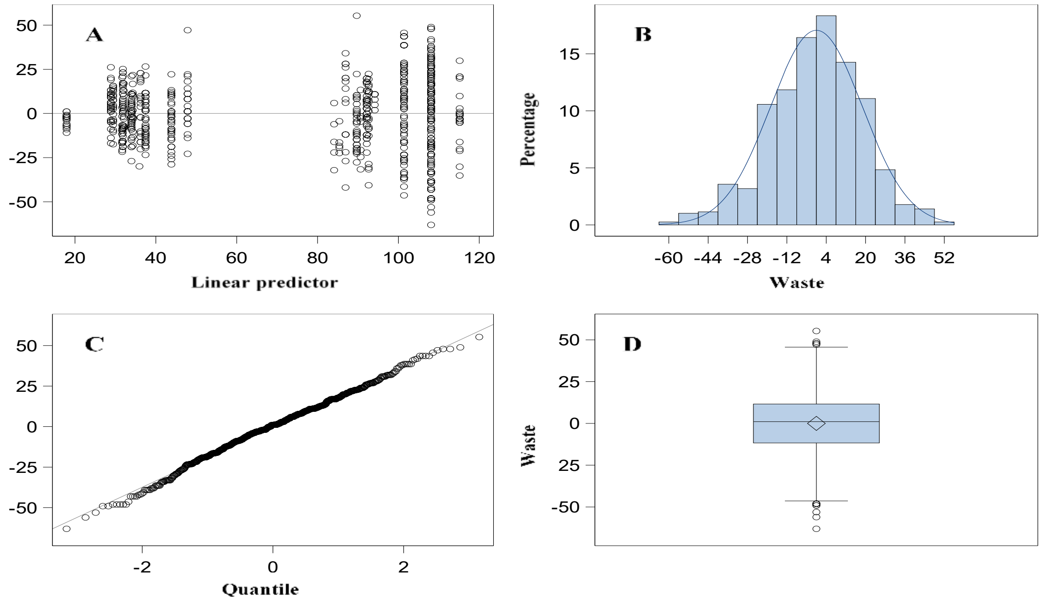

Figure 4: (A) Residuals vs. Linear Predictor, (B) residual histogram, (C) normal probability plot (QQ), (D) residual boxplot

In the QQ normal probability plot, most points align closely along the diagonal reference line. However, at the extremes of the distribution, slight deviations from the line are observed, which do not affect the normal behaviour of the residuals. In the QQ normal probability plot, most points align closely along the diagonal reference line (Figure 4C). Some outliers may be slightly affecting the model results (Figure 4D).

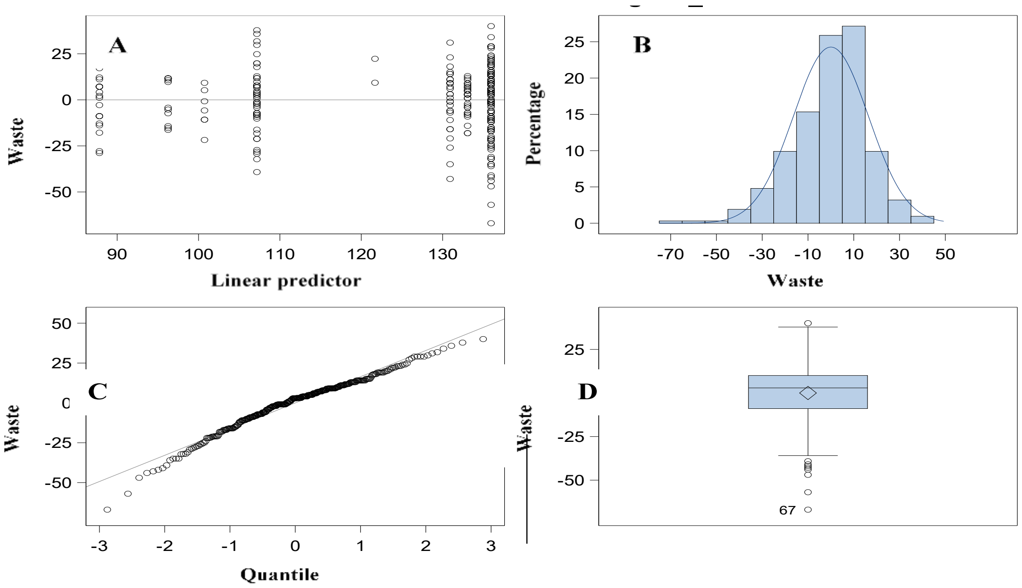

Figure 5: Residual plots of the model corresponding to fruit length, where (A) represents Residuals vs Linear Predictor. (B) Residual histogram. (C) Normal Probability Graph (QQ). (D) Residual Boxplot.

The analysis of the effect of fruit length is somewhat similar to that of flowers, as the scatter plot is not uniform, resulting in heteroscedasticity (Figure 5A). The residual histogram suggests that the assumption of normality of the residuals is reasonably well met (Figure 5B). The normal probability plot, like the previous one, shows the points aligned with the reference line, indicating that the assumption of normality of the residuals is moderate (Figure 5C). Finally, the box plot shows that the median of the residuals is very close to zero, indicating a good result. However, there are some outliers in the data (Figure 5D).

4.3. Herbivory index (% of leaf damage)

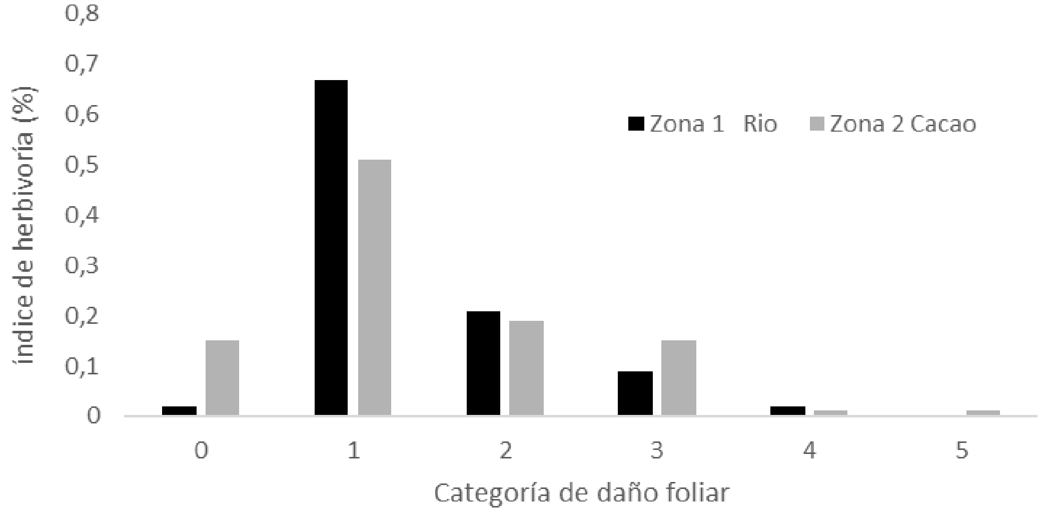

Figure 6: Herbivory index in river margin areas and cocoa crop margins

In Figure 6 the leaves were analyzed from the 20 of the Piper sp. species in the study areas, it was observed that all individuals had some percentage of foliar damage, with category 1 (1-6%) being the most representative in both study areas with a percentage of 0.67 (zone 1) and 0.51 (zone 2), respectively. Conversely, the category that presented the lowest percentage of foliar damage was 5 (51-100%) with values close to zero in both study areas.

Table 2: ***Herbivory indices by foliar damage category in the river margin and cacao cultivation areas. G = 31.02, df = 5, P < 0.001.***

Foliar damage category (%)	Frequency	Zone 1, River	Zone 2, Cacao	Total
0 (0%)	Observed	29	4	33
	Expected	16.50	16.50	
1 (1–6%)	Observed	102	133	235
	Expected	117.50	117.50	
2 (7–12%)	Observed	37	42	79
	Expected	39.50	39.50	
3 (13–25%)	Observed	29	17	46
	Expected	23.00	23.00	
4 (26–50%)	Observed	2	4	6
	Expected	3.00	3.00	
5 (51–100%)	Observed	1	0	1
	Expected	0.50	0.50	
Total		**200**	**200**	**400**

In Table 2, when determining the differences between the distributions of the study areas according to the foliar damage categories, statistically significant differences were found ($\chi^2 = 31.02$, df = 5, P < 0.001). In group zone 1 (River), a higher percentage of values with a scale between 0 and 3 was observed, while in group zone 2 (Cacao), there was a higher percentage of values with a scale of 1. No significant differences were detected between the average values of zone 1 and zone 2 (P >0.05, F= 0.07).

5. DISCUSSION

5.1. Reproductive Traits of Piper Sp. Across Contrasting Habitats

The results of this study indicate that reproductive traits of *Piper* sp., specifically the length of inflorescences and infructescences, were not significantly different between riparian habitats and the edges of cacao cultivation systems. However, plant height and the degree of reproductive maturity showed significant relationships with inflorescence length, suggesting that intrinsic plant characteristics play a stronger role in determining reproductive trait expression than the environmental differences between the studied habitats. These findings are consistent with the idea that plant ontogeny and growth conditions strongly influence trait expression in plants (Gómez-Fernández & Milla, 2022). As plants increase in size and age, they often allocate more resources to reproductive structures, which may explain the observed relationship between plant height and inflorescence length.

Although the total number of inflorescences and fruits differed between the two sites, these differences may be linked to variations in plant maturity or microenvironmental conditions rather than herbivory itself. Riparian habitats are typically characterized by higher soil moisture and dynamic light environments due to canopy gaps and proximity to water bodies. In contrast, agroforestry systems such as cacao plantations often present more stable but shaded microclimates (Quiroz-Pacheco et al., 2020). These differences in light availability and resource allocation could influence plant growth and reproductive output. Similar habitat-driven variation in plant reproductive traits has been reported in forest edge systems, where microclimatic gradients strongly affect plant performance and reproductive investment (Wirth et al., 2008).

5.2. Herbivory Patterns and Environmental Influences

The analysis of foliar damage revealed that all sampled individuals of *Piper* sp. experienced some degree of herbivory, although most leaves fell within the lowest damage category (1–6% leaf removal). This pattern suggests relatively low herbivory intensity in the studied populations. The dominance of low damage categories is consistent with observations in many tropical plant species, where plants maintain effective defensive strategies that limit extensive herbivore damage despite high herbivore diversity.

Interestingly, although riparian habitats are often associated with higher biodiversity and potentially greater herbivore abundance, the results did not show a statistically significant difference in the herbivory index between the two study areas. This suggests that environmental conditions alone may not fully explain patterns of herbivore damage in *Piper* species. Instead, intrinsic plant traits such as chemical defenses or leaf structural characteristics may play an important role in regulating herbivore activity. Previous research has demonstrated that many species of *Piper* produce bioactive secondary metabolites with insecticidal or repellent properties, which can reduce herbivore pressure (Divekar et al., 2022; Gonçalves et al., 2022). These chemical defenses may help explain the relatively low levels of foliar damage observed in both habitats.

Environmental factors, particularly light availability, may also influence plant defense mechanisms. Studies have shown that sunlight exposure can alter the production of secondary metabolites, potentially increasing plant resistance to herbivores (Assunção et al., 2023). Increased solar radiation can stimulate the synthesis of phenolic compounds and other defensive metabolites that reduce leaf palatability and herbivore feeding activity (Darko et al., 2022; Marín et al., 2022). Such physiological responses may partly explain why riparian plants, which are often exposed to higher light levels due to more open canopy structures, tended to exhibit slightly lower levels of foliar damage compared with individuals growing in the shaded cacao agroforestry system.

5.3. Relationship Between Herbivory and Reproductive Traits

Contrary to expectations, the results of this study did not reveal a significant relationship between the herbivory index and the reproductive traits measured in *Piper* sp. individuals. This suggests that the levels of foliar damage observed were insufficient to produce measurable effects on reproductive investment. In many plant species, moderate levels of herbivory can be tolerated without substantial reductions in reproductive output because plants are able to compensate for tissue loss through physiological adjustments or resource reallocation.

The absence of a strong relationship between herbivory and reproductive traits in this study aligns with previous research indicating that herbivore damage does not always translate into reduced reproductive performance (Müller et al., 2023). In some cases, herbivory may primarily affect leaf traits or photosynthetic capacity without directly altering the development of reproductive structures. Furthermore, plants may exhibit compensatory responses that allow them to maintain reproductive output even under moderate herbivore pressure.

Nevertheless, the interaction between herbivory and plant reproduction is complex and context-dependent. Some studies have reported that herbivory can stimulate increased flowering as a compensatory or defensive strategy (Peschiutta et al., 2020). In contrast, others have found negative effects on fruit and seed quality when herbivore damage is severe. In the present study, the low overall herbivory levels may have limited the ability to detect such effects, particularly given the relatively small sample size and the observational nature of the study.

5.4. *Ecological Implications*

The findings of this research contribute to a broader understanding of plant–herbivore interactions in tropical ecosystems. The relatively low herbivory levels observed in *Piper* sp. populations suggest that plant defensive mechanisms may effectively regulate herbivore pressure in both riparian and agroforestry environments. Additionally, the lack of strong differences in herbivory between habitats indicates that agroforestry systems such as cacao plantations may still maintain ecological processes similar to those occurring in nearby natural habitats.

This is particularly relevant for tropical landscapes where natural forests increasingly coexist with agricultural systems. Agroforestry systems are often considered biodiversity-friendly land-use strategies because they can preserve elements of forest structure and support diverse ecological interactions. The presence of *Piper* species in both habitat types and the similar herbivory patterns observed suggest that these plants may play a role in maintaining ecological connectivity between natural and managed ecosystems.

6. LIMITATIONS

Despite providing useful insights into herbivory patterns in *Piper* species, this study has several limitations that should be considered when interpreting the results. The relatively small sample size and the limited spatial scale of sampling may reduce the ability to detect subtle ecological patterns. Additionally, herbivory was assessed using visual estimates of leaf damage, which, although widely used, may introduce some degree of subjectivity.

7. CONCLUSION

This study found no statistically significant relationship between foliar herbivory and the reproductive functional traits of Piper sp. across the two studied habitats, suggesting that the levels of herbivore damage observed were insufficient to produce measurable effects on reproductive investment. Nevertheless, sunlight availability emerged as an important contextual factor. Furthermore, Piper sp. plants located along the riverbank were more exposed to high levels of sunlight, exhibiting a lower herbivory rate than those in the agroforestry system, but showing a slight increase in foliar consumption by folivores. However, the analysis of the results shows that the difference in herbivory percentage between the two sites is not statistically significant, which could be due to the insects' generalist nature. Similarly, the number and length of reproductive structures are not related to increases or decreases in herbivory. Inflorescence length was associated with both plant height and reproductive maturity stage, with taller plants and more advanced reproductive stages producing longer inflorescences. In regard to the research questions that directed this study: No difference in the mean herbivory intensity was found between the riparian and cacao agro forest habitats. Similalrey, there was neither a significant relationship, between the herbivory index and inflorescence or infructescence length; nor was there a significant relationship between the inflorescence length and the height of the plants, nor did this relationship differ significantly between the habitat types.

8. FUTURE RESEARCH DIRECTIONS

Future research could expand on these findings by incorporating larger sample sizes, multiple seasons of sampling, and a broader range of environmental conditions. Investigating additional plant functional traits, such as leaf chemical composition or structural defenses, could also provide deeper insight into the mechanisms regulating herbivory in *Piper* species. Moreover, studies integrating insect community surveys would help clarify how herbivore diversity and feeding guilds influence herbivory dynamics in tropical plant communities.

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