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Plant species richness, not hygrothermal stress, is the main predictor of gall-inducing insect richness in Peruvian Amazon forests

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Abstract

Patterns of gall-inducing insect diversity tend to be influenced by both habitat-related and plant-related characteristics. We investigated the distribution patterns of galling insects in four vegetation types (*terra firme* forest, white-sand dry forest, white-sand wet forest and palm swamp forest) of the Peruvian Amazon to test if the insect gall diversity 1) differs among different types of vegetation and 2) depends on host plant richness. In total, we found 11,579 galls belonging to 249 insect gall morphotypes, distributed across 30 botanical families and 75 plant species. Among host plant families, Fabaceae showed the greatest richness of insect gall morphotypes. We found that galling species richness was lower in palm swamp forest than in white-sand forests, which can be explained by the lower richness of plants in this type of vegetation. However, we found no evidence of greater richness in xeric habitats (e.g., white-sand dry forest) than in more mesic vegetation (*terra firme* forest), contradicting the hypothesis of hygrothermal stress. We also found that plant species richness was positively influenced with the richness and abundance of galling species, regardless of vegetation type. Galling insect species composition differed significantly between vegetation types, similarly to the floristic composition. Our findings show that the diversity of galling insects in the tropical rainforests of Peruvian Amazon are mainly influenced by host plant composition and host plant richness.

Keywords: habitat effects, insect galls, plant-insect interaction, rain forest

INTRODUCTION

The diversity of plant species and herbivorous insects is very high in humid tropical forests (Slade & Ong, 2023). However, a guild of herbivorous insects that is still poorly studied in humid tropical forests, especially in the Amazon rainforest, is the group of gall-inducing insects (Julião et al., 2014a). The galling insects are highly specialized herbivores, capable of causing internal damage to the structure and physiology of plants, inducing the growth of abnormal structures in vegetative tissues via hypertrophy and /or hyperplasia (Shorthouse et al., 2005). These structures are known as galls. Several hypotheses have been proposed to explain differences in species diversity of galling insects between sites, mainly concerned with floristic diversity and habitat characteristics (Fleck & Fonseca, 2007; Miller III & Raman, 2018).

The plant richness hypothesis is widely accepted as an explanation for the distribution patterns of gall-inducing insects (Fleck & Fonseca, 2007). This hypothesis suggests that the richness of host plants directly influences the diversity of gall-inducing insects (Araújo, 2013; Araújo et al., 2013; Oyama et al., 2003), because each species of plant represents a potential niche for galling insects (Mendonça, 2007). Various studies provide evidence corroborating the plant richness hypothesis. For example, Araújo (2013) in a meta-analysis found that plant species richness strongly affects galling insect species richness, regardless of the geographic region and scale of the study. In an earlier work, Cuevas-Reyes et al. (2004) showed that plant species richness influences gall-inducing insect species richness in two types of habitats (deciduous and riparian) in the dry tropical forests of Mexico. For humid tropical forests, which are among the most diverse in plant species worldwide (ter Steege et al., 2013), few studies have assessed the effect of plant diversity on the distribution of gall-inducing insects (Julião et al., 2014a).

Another leading explanation for patterns of galling insect diversity, is the hygrothermal stress hypothesis (Fernandes & Price, 1988), which predicts that gall-inducing insect diversity should be greater in stressful habitats that are characterized by the limited availability of water and soil nutrients (Price et al., 1998). The main mechanisms responsible for the high galling species richness in stressed environments are thought to be related to nutritional flexibility and relationships with natural enemies (Fernandes & Price, 1988; Fleck & Fonseca, 2007). Plants under environmental stress tend to be more sclerophyllous (Fagundes et al., 2020; Poorter et al., 2009) and accumulate higher levels of chemical compounds (Fagundes et al., 2018; Leite et al., 2022). Galling insects have adaptive advantages in xeric habitats because they sequester secondary metabolites in gall tissue as a mechanism of protection against natural enemies (Stone & Schönrogge, 2003). Internally feeding gall-inducing insects attacking such plants would experience greater protection from their natural enemies than free-living herbivores (Gonçalves-Alvim & Fernandes, 2001), thus leading to a greater diversity of insect galls. Additionally, the stressful conditions of xeric environments reduce the occurrence of natural enemies, such as pathogens, predators, and parasitoids (Fernandes & Price, 1988). Consequently, the survival rate of gall-inducing insects tends to be higher in xeric environments than in mesic environments. Traditionally, the tests for the hypothesis of hygrothermal stress are done by comparing different types of vegetation (Cuevas-Reyes et al., 2004; Gonçalves-Alvim & Fernandes, 2001; Wright & Samways, 1998), but few studies have investigated whether stress levels and predictions of the stress hypothesis apply to different types of rainforests.

Peru is the second-largest Amazonian country in terms of forested area, totaling 778,451 km^2 (Rojas & Castaño, 1990). This area is composed of a variety of vegetation types (Tuomisto et al., 1995), which represents a great diversity of potential niches for herbivorous arthropods, such as gall-inducing insects (Mendonça, 2007). The flora of the Peruvian Amazon is characterized by an array of vegetative formations habitats (Tuomisto et al., 1995). Fluctuations in water level, as well as different nutrient concentrations and soil physical properties, promote the development of diverse strategies and adaptations among plant species (Draper et al., 2018; Fine et al., 2010; Nebel et al., 2001). White-sand forests, for instance, have nutrient-poor and highly acidic soil, and are characterized by sclerophyllous vegetation, mono-dominance, high endemism, and low diversity, with a closed canopy dominated by thin-stemmed woody species (Fine et al., 2006). Based on species composition, canopy height, and soil drainage, these forests can be classified as wet or dry white-sand forests (Encarnación, 1993). Palm swamp forest ecosystems are characterized by periodic flooding, and accumulate water from precipitation due to poor soil drainage or rare events of severe flooding along rivers (Junk et al., 2011). They are usually dominated by one or more palm species, most commonly *Mauritia flexuosa* L. (Arecaceae) (Draper et al., 2018). These forests are characterized by low diversity, with plant species adapted to strongly seasonal hydrological influences (Pitman et al., 2014). On the other hand, *terra firme* forests present an extremely diverse and heterogeneous flora, with soils rich in nutrients, and a wide availability of niches and ecological resources (Pitman et al., 2001).

In the present study, we compared the diversity of galling insects in four forest vegetation types in the Peruvian Amazon, characterized by distinct plant communities and soils of different hydric and nutritional conditions (Draper et al. 2018; Quesada et al., 2011).

Based on previous studies (Quesada et al., 2011, 2012), Amazonian forests can be ranked in a soil fertility gradient in the direction *terra firme* forest > palm swamp forest > white-sand wet forest > white-sand dry forest. On the other hand, considering the level of soil moisture, the gradient is different where palm swamp forest > white-sand wet forest > *terra firme* forest > white-sand dry forest. Therefore, white-sand dry forest is the type of vegetation expected to be the most stressed (i.e. xeric), as it is associated with soil that is the poorest in nutrients and water (Figure 1). Thus, we tested the following hypotheses: (1) Habitats with higher hygrothermal stress should have higher species richness and abundance of gall-inducing insects than less-stressful habitats, as predicted by hygrothermal stress hypothesis (Fernandes & Price, 1988), and, (2) Plant species richness positively affects the diversity of gall-inducing insects, as predicted by the plant richness hypothesis (Araújo, 2013). Consequently, we expect a higher richness and abundance of galling insects in more xeric forest (white-sand dry forest) than in other vegetation types. We also expected a positive relationship between host plant species richness and species richness and abundance of gall-inducing insects. Additionally, we also tested whether the composition of gall-inducing insects differs among different vegetation types, reflecting the high specialization of gall-inducing insects on their host plants.

METHODS

Study area

The study site was situated southwest of the city of Iquitos, in the province of Loreto in the Peruvian Amazon, within the Quistococha Regional Reserve (S 03° 49.786′ W 073° 19.333′) and Allpahuayo-Mishana National Reserve (S 03° 58.034′ W 073° 25.138′) (Figure 2). The elevation at the two sites was 104 and 120 m above sea level. The climate is tropical, characterized by a mean annual temperature of 26°C and an average annual rainfall of 3,087 mm (Marengo, 1998). The Allpahuayo-Mishana National Reserve presents extremely variable edaphic conditions, with soils that vary in texture from clay to almost pure sand, and in drainage from waterlogged swamps to well-drained hill tops (Vormisto et al., 2000). In contrast, Quistococha Regional Reserve has poorly drained soils that are often flooded (Encarnación, 1985), with vegetation dominated by the palm *Mauritia flexuosa* (Draper et al., 2018). Overall, 32 sampling plots were established, of which 24 were in the Allpahuayo-Mishana National Reserve (8 plots in *terra firme* forest, 8 plots in white-sand wet forest, 8 plots in white-sand dry forest) and 8 plots were in the Quistococha Regional Reserve (all in palm swamp forest).

Sampling of galling insects and host plants

To determine the area for setting up the plots, we conducted a thorough analysis of the four vegetation types. Factors such as terrain topography, plant species diversity, and tree distribution at different densities were taken into consideration. Subsequently, our sampling was undertaken bi-monthly between December 2021 and June 2022. In each vegetation type, we established 8 plots of 5 x 20 m, spaced at 20 m intervals, totaling 0.08 ha sampled for each site, in accord with the methodology proposed by Julião et al. (2014b). In each plot, all trees with a diameter at breast height (dbh at 1.3 m height) equal to or greater than 10 cm were measured and collected, using standard methods described in the RAINFOR protocol (Phillips et al., 2009). The plant species sampled in each plot have been identified previously by botanical specialists and their identifications were downloaded via the ForestPlots.net online database (ForestPlots.net, 2021; Lopez-Gonzalez et al., 2011). All the plots were established in the understory vegetation and then visually projected on the canopy, delimiting the sampling area to collect the tree crowns located in the layer above each individual. Subsequently, 10 terminal units of the plant were randomly collected by climbing and with a 10 m telescoping aluminum pole pruner. In the field, insect gall morphotypes were recorded, together with their abundances, on each individual tree. Gall morphotypes were characterized by external morphology, shape, color, presence of trichomes, number of chambers, and the host plant organ attacked, as proposed by Isaias et al. (2014).

Data analyses

In order to test whether distinct vegetation types differ in terms of environmental stress, we conducted a comparative analysis of soil nutrient levels among different habitats. Utilizing data from Quesada et al. (2011, 2012), collected in the same locations of present study, we compared nutrient levels including Al, Ca, K, Mg, Na, N, C, and pH across *terra firme* forest, white-sand dry forest, and white-sand wet forest. It's important to note that due to data constraints, soil nutrient information for the palm swamp forest was not available for this study. Generalized Linear Models (GLMs) with a Gaussian error distribution were constructed to assess variations in soil nutrient values among the vegetation types. In these models, soil nutrient values were considered as the response variable, whereas vegetation types, soil types, and the interaction term between vegetation types × soil types were considered as explanatory variables. Furthermore, *post hoc* contrast tests were performed to elucidate specific differences in soil nutrient compositions between the different vegetation types.

To test if the species richness and abundance of gall-inducing insects are influenced by the vegetation type and plant species richness we fitted generalized linear mixed models (GLMMs). In these GLMMs, vegetation types, total plant species richness (number of nonhost and host species trees), and the interaction term between total plant species richness × vegetation types were considered as fixed effects, whereas the plots were included as a random effect variable. We used a Poisson error structure (count data) with the log-link function for the galling species richness model. For galling insect abundance (count data) the model was overdispersed so a negative binomial error structure was used. We also used a GLMMs to compare if the plant species richness differs between the vegetation types, using a Poisson error distribution. The GLMMs for plant species and galling species richness were constructed using the *glmer* function, while for the abundance of galling species, the *glmer.nb* function was employed within the *lme4* package (Bates et al., 2023). Post hoc pairwise comparisons were made using Tukey's HSD test (R function *glht* from the R package *multcomp*, Hothorn et al., 2008), to highlight the differences in galling species richness and abundance, as well as plant species richness, among the different vegetation types. Chi-square tests and p-values were calculated using the Anova function in the package *car* (Fox & Weisberg, 2019).

To test differences in the galling insect composition between the different vegetation types, we carried out analyses of non-metric multidimensional scaling (NMDS). Prior to NMDS analyses, we removed disconnected plots that did not share species with other plots in the sampled vegetation types, using the function *disconnected* in the *vegan* package (Bell et al., 2018). In the case of floristic composition five *terra firme* plots were removed (plots removed: 5/8); for galling species composition, six *terra firme* plots were removed (plots removed: 6/8), along with two plots of palm swamp (plots removed: 2/8) and one plot of white-sand dry forest (plots removed: 1/8). The tests were also conducted using all the data for comparison. To test for differences in species composition among both plants and galling insects we used Bray-Curtis distance metrics, based on abundance data. A nonparametric permutation procedure (ANOSIM) was then applied using the Bray-Curtis index with 999 permutations, to test the significance of groups formed in the NMDS (Hammer et al., 2001).

We also employed an individual-based abundance rarefaction methodology using the *iNEXT* package (Hsieh et al., 2016) to assess the extent to which our sampling recorded the species within each vegetation type. This analysis enabled us to visualize species accumulation relative to the number of individuals sampled, offering insights into the effectiveness of our sampling. All statistical analyses were performed using R software version 4.2.2 (R Core Team, 2022).

RESULTS

We found a total of 11,579 galls belonging to 249 insect gall morphotypes on 75 species of host plants distributed among 30 botanical families (Table S1). The plant families that showed the greatest richness of insect galls were Fabaceae, with 47 (18.9%) morphotypes, Calophyllaceae with 20 (8%), and Euphorbiaceae with 18 (7.2%) morphotypes. The most important host plant species were *Tapirira guianensis* with 16 (6.4%), *Caraipa utilis* with 13 (5.2%), *Micrandra elata* with 12 (4.8%), *Eschweilera coriacea* with 11 (4.4%), and *Sloanea parvifructa* with 10 (4%) insect gall morphotypes (Table S2).

The total species richness of plants varied significantly among different vegetation types ($\chi2 = 16.30$, $Df = 3$, $p < 0.001$). The palm swamp vegetation had the lowest total plant richness (mean ± SD: 2.13 ± 0.99), but the other vegetation types did not differ (Figure S1). Most soil attributes (Ca, C, Mg, K, Na, N, and pH) did not differ among the studied vegetations ($p > 0.05$; Figure S2). Only the level of Al ($p < 0.01$) was higher for the *terra firme* forest compared to other vegetation types (white-sand dry and wet forests).

We found that galling species richness varied significantly among the types of vegetation ($\chi 2 = 10.88$, $Df = 3$, $p = 0.01$; Table 1). Palm swamp vegetation exhibit the lowest richness compared to the other vegetation types, which showed no significant differences (Figure 3). Comparing the rarified richness of galling insects between the vegetation types was observed higher values for the *terra firme* vegetation and lower for the palm swamp vegetation (Figure S3). On the other hand, galling insect abundance did not differ between vegetation types ($\chi 2 = 6.93$, $Df = 3$, $p = 0.07$; Table 1). Total plant species richness positively influenced galling species richness ($\chi 2 = 20.56$, $Df = 1$, $p < 0.001$; Table 1, Figure 4) and galling insect abundance ($\chi 2 = 11.75$, $Df = 1$, $p < 0.001$; Table 1, Figure 5), regardless of vegetation type. Furthermore, galling species richness was influenced by the interaction of total plant species richness and vegetation types ($\chi 2 = 10.73$, $Df = 3$, $p = 0.01$; Table 1), but not by the abundance of galling insects.

Plant species composition differed significantly between the vegetation types (Stress = 0.0776, R = 0.827, $p < 0.001$, Figure 6a). We found that palm swamp and *terra firme* forest plots differed most in floristic composition. Similarly, the composition of gall-inducing insect species differed significantly between vegetation types (Stress = 0.0645, R = 0.839, $p < 0.001$, Figure 6b), with the greatest differences observed between palm swamp and *terra firme* forest plots. Furthermore, we also observed a significant overlap between vegetation types and the plots when including both connected and disconnected plots for plant species and gall-inducing insect species composition (Figure S4; Tables S3 and S4, respectively).

DISCUSSION

In the present study, we assessed the occurrence of host plants and gall-inducing insects in different types of forest vegetation in the Peruvian Amazon, a megadiverse and under-sampled region. Our results show that the studied vegetations differed little in terms of soil nutrients, contrary to the expected pattern (Draper et al., 2018; Quesada et al., 2011). Similarly, the total plant richness also varied minimally among different forest types, with the swamp forest being the only exception, exhibiting lower richness than the others (white-sand wet, white-sand dry and *terra firme* forests). Regarding gall-inducing insect richness, we observed that the palm swamp forest had a lower number of species than the other vegetations (white-sand wet and dry forests), reflecting the variation in plant species richness. In line with our expectations, the richness of plant species positively influenced both the richness and abundance of gall-inducing insects. Thus, our findings do not provide evidence for a well-defined stress gradient among the studied vegetations, considering soil nutrients, plant species richness and galling species richness.

Previous studies testing the hygrothermal stress hypothesis (Fernandes & Price, 1988) have found higher galling species richness in xeric habitats than in mesic habitats in tropical forests (Cuevas-Reyes et al., 2004; Julião et al., 2014b) This pattern has been observed in other Brazilian Amazon (Julião et al., 2014b), Neotropical savannas (Gonçalves-Alvim & Fernandes, 2001; Lara & Fernandes, 1996; Lara et al., 2002), and in other ecosystems worldwide (Cuevas-Reyes et al., 2004; Fernandes & Price, 1988; Wright & Samways, 1998). These previous studies often contrasted very different vegetation types in terms of soil fertility and moisture (Cuevas-Reyes et al., 2004; Julião et al., 2014b). As previously presented, our results do not support consistent differences in stress among the studied vegetations, considering soil attributes. Based on previous studies (Draper et al., 2018; Quesada et al., 2011), we expected a stress gradient ranging from *terra firme* (less stressed environment) to white-sand dry vegetation (more stressed environment). On the other hand, we found that the levels of important macronutrients for soil fertility (Ca, C, k, Mg, Na, and N) did not differ among the *terra firme*, white-sand wet, and white-sand dry areas, and only the level of Al differed among the vegetation types, being higher for the *terra firme* forest. The likely low difference in soil characteristics among the vegetation types probably reflected in plant richness, which also did not differ between *terra firme* and white-sand dry vegetation areas. As previously discussed, only the palm swamp vegetation had significantly lower richness compared to the other vegetations. These results suggest that, for tropical forests, soil flooding levels may be an important environmental factor, limiting the occurrence of some plant species.

Contrary to initial expectations, the richness and abundance of gall-inducing insects were not higher in the white-sand dry vegetation than in *terra firme f*orest. On the other hand, our results showed that the richness of gall- inducing insects in the palm swamp forest was lower than in the white-sand forests. We believe that the main explanation for this is that palm swamp forest exhibited lower plant species richness compared to other vegetation types. Palm-dominated ecosystems are known for their unique ecological characteristics, which could shed light on this disparity (Pitman et al., 2014). The reduced presence of galling species within the palm swamp forest might be attributed to the limited diversity of host plants specific to this habitat (Draper et al., 2018). Additionally, the overall lower diversity of susceptible plant species within the palm swamp forest could contribute to the low number of galling insect species.

Our findings also show that galling insect diversity was positively influenced by plant species richness in different vegetation types of the Peruvian Amazon. These results are in line with the pattern observed in previous studies (e.g., Cuevas-Reyes et al., 2004; Gonçalves-Alvim & Fernandes, 2001; Wright & Samways, 1998). Plant species richness is postulate as the main factor of plant assemblages that can influence galling communities (review in Araújo, 2013); the greater the number of plant species, the more potential niches (i.e., hosts) open up for gall-inducing species (Cuevas-Reyes et al., 2004). Our results supported the hypothesis of plant richness, both through the positive correlation of this factor with the richness of galling insects observed for all studied vegetation types, and by the low richness of galling insects in the palm swamp forest, which was also the vegetation poorest in plants.

The composition of gall-inducing insect guilds varied greatly between vegetation types. The greatest differences were observed between palm swamp and *terra firme* forests, both in plant and galling insect composition. These differences reflect the divergence between these vegetation types, which differ in floristic diversity, plant structure, and soil moisture (Draper et al., 2018). Our finding corroborates previous studies that point to divergent gall-inducing insect composition across tropical rain forests (e.g., Julião et al., 2017). Additionally, the dissimilarity in galling fauna can be explained by the presence of different species super-hosts plants (review in Grandez-Rios et al., 2020), which can greatly increase the number of species of gall-inducing insects, regardless of the number of plant species (Araújo et al., 2014; Veldtman & McGeoch, 2003). Although we did not test this, we observed that the super-host plants differed between each type of forest (see Table S2). The presence of super-host plants further indicates that the composition of plant assemblages is important for the galling community (Araújo et al., 2013). Our findings indicate that the diversity of gall-inducing insect guilds is influenced by not only the richness of host plants, but also the taxonomic composition of plant communities, reinforcing the findings of previous studies (Araújo et al., 2013; Fernandes et al., 2010).

The plant family exhibiting the highest gall richness was Fabaceae, with 47 morphotypes, also boasting the largest number of host species (twelve species in total). A compilation of key studies conducted in the Brazilian Amazon region emphasizes the pivotal role of Fabaceae as the primary host family in Amazonian forests (Julião et al., 2014a; Proença & Maia, 2023). The great intrinsic galling insect richness of this plant family may be due to the great diversity of species it presents (Mendonça, 2007). No reports exist in the literature regarding the high gall diversity observed in plant species on *Tapirira guianesis*, *Caraipa utilis*, *Micrandra elata*, *Eschweilera coriacea*, and *Sloanea parvifructa*—identified as the most significant host species in our study.

To the best of our knowledge, this is the first study investigating patterns of galling insect diversity in the Peruvian Amazon, which is one of the most diverse tropical ecosystems on the planet. Our findings reinforce the importance of plant richness in determining galling insect diversity in this ecosystem. Furthermore, it could be argued that the emphasis on environmental stress does not align with our findings regarding the distribution of gall-inducing insects. It's possible that other factors, such as plant architecture or the presence of super-host taxa, might be more relevant or complementary in explaining this diversity.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

JMGR ─ Conceptualization, Data curation, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing; JMGR and WSA ─ Formal Analysis; WSA and VCM ─ Conceptualization, Methodology, Supervision, Writing – review & editing; APB, ENHC, TRB, RVM, AMM, RGV, GFL and JRH — Data collection.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.0vt4b8h5z (Grandez-Rios et al., 2024)**.**

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Table 1 Results of GLMMs models assessed the influence of total plant species richness, vegetation types (*terra firme* forest, white-sand dry forest, white-sand wet forest and palm swamp forest), as well as their combined effect, on richness and abundance of galling insects in the Peruvian Amazon.

	Richness of galling species			Abundance of galling species		
	χ2	*Df*	*p*	χ2	*Df*	*p*
Total plant species richness	20.56	1	< 0.001	11.75	1	< 0.001
Vegetation types	10.88	3	0.01	6.93	3	0.07
Total plant species richness: Vegetation types	10.73	3	0.01	6.45	3	0.09

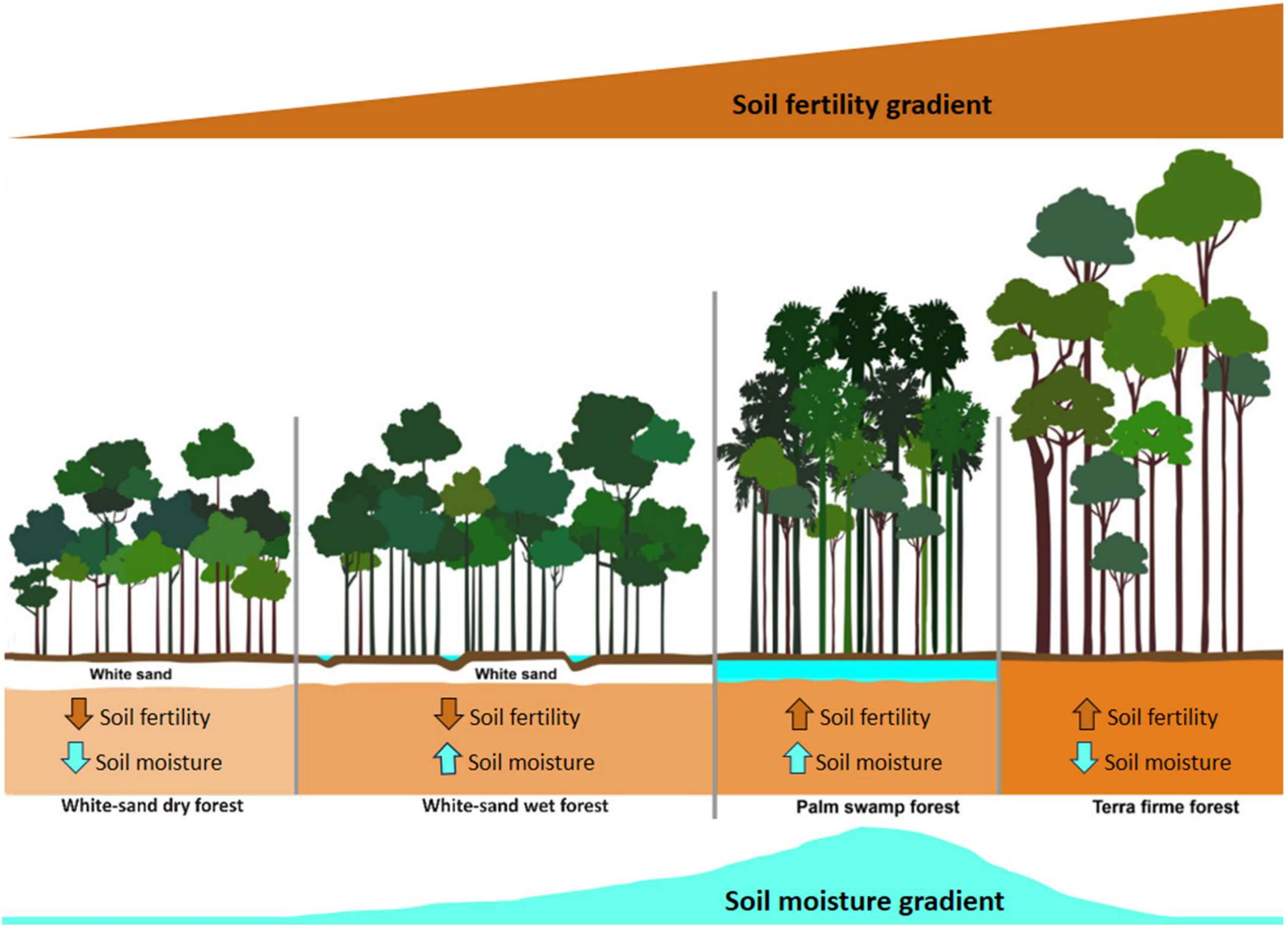

Figure 1 A conceptual model for the environmental differences in soil fertility and moisture among vegetation types in the Peruvian Amazon. Concerning soil fertility, an environmental gradient is anticipated in the following order: *terra firme* forest > palm swamp forest > white-sand wet forest > white-sand dry forest. Conversely, when considering soil moisture levels, the gradient differs, with palm swamp forest > white-sand wet forest > *terra firme* forest > white-sand dry forest.

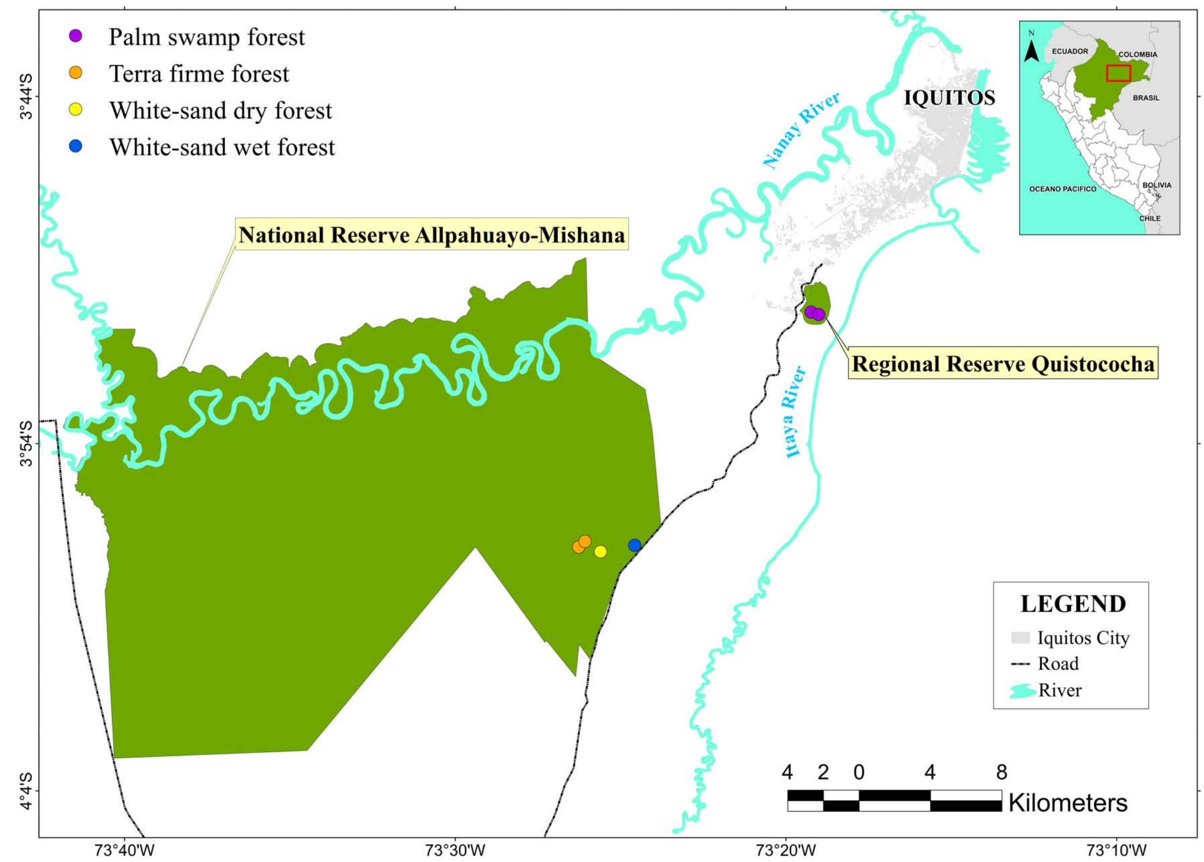

Figure 2 Map of sampling areas in four vegetation types in the National Reserve Allpahuayo-Mishana and Regional Reserve Quistococha, Peru.

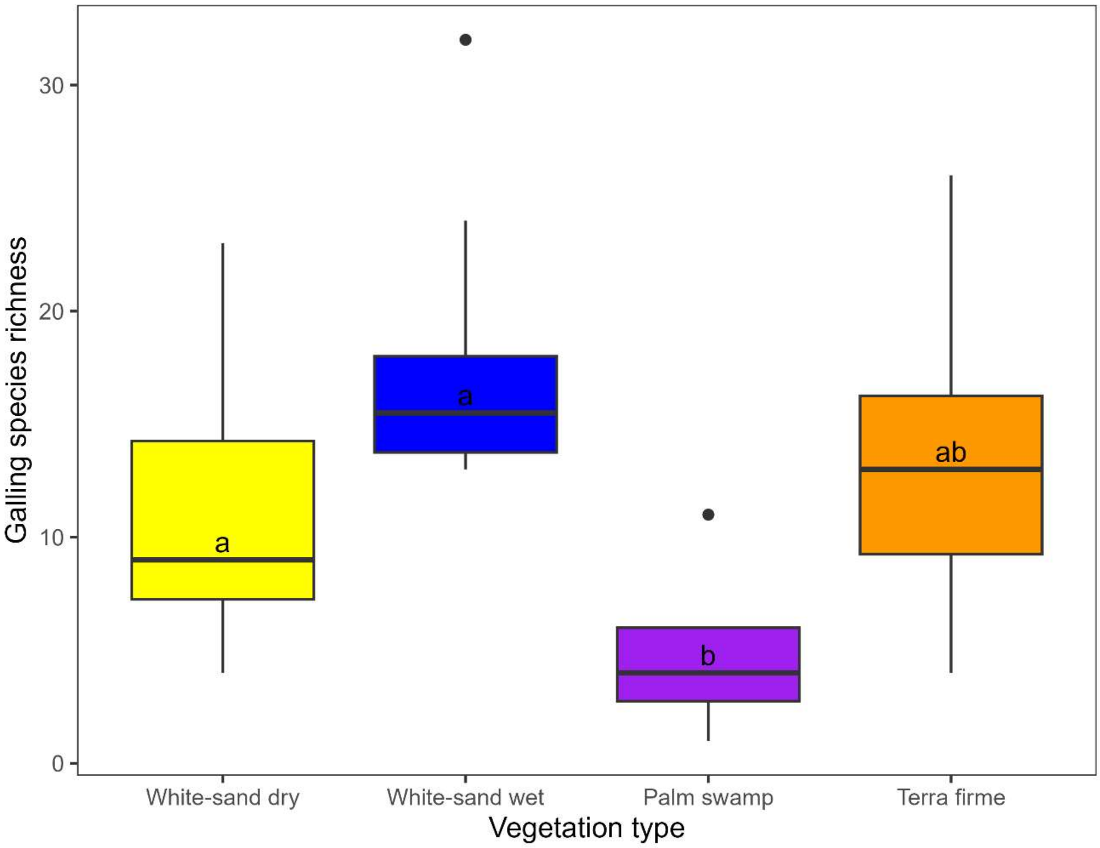

Figure 3 Comparison of galling species richness between different vegetation types in the Peruvian Amazon. Different letters represent significant differences ($p < 0.05$).

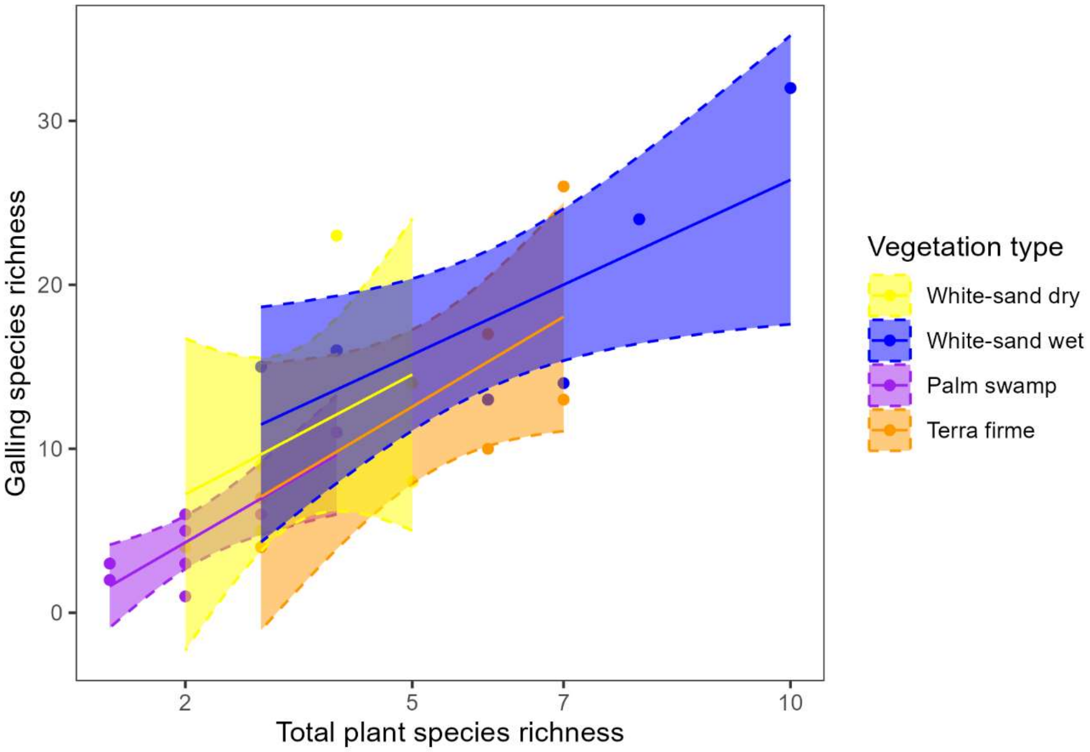

Figure 4 Relationship between galling species richness and total plant species richness in plots sampled in different vegetation types in the Peruvian Amazon. The dotted lines represent the model’s 95% confidence intervals.

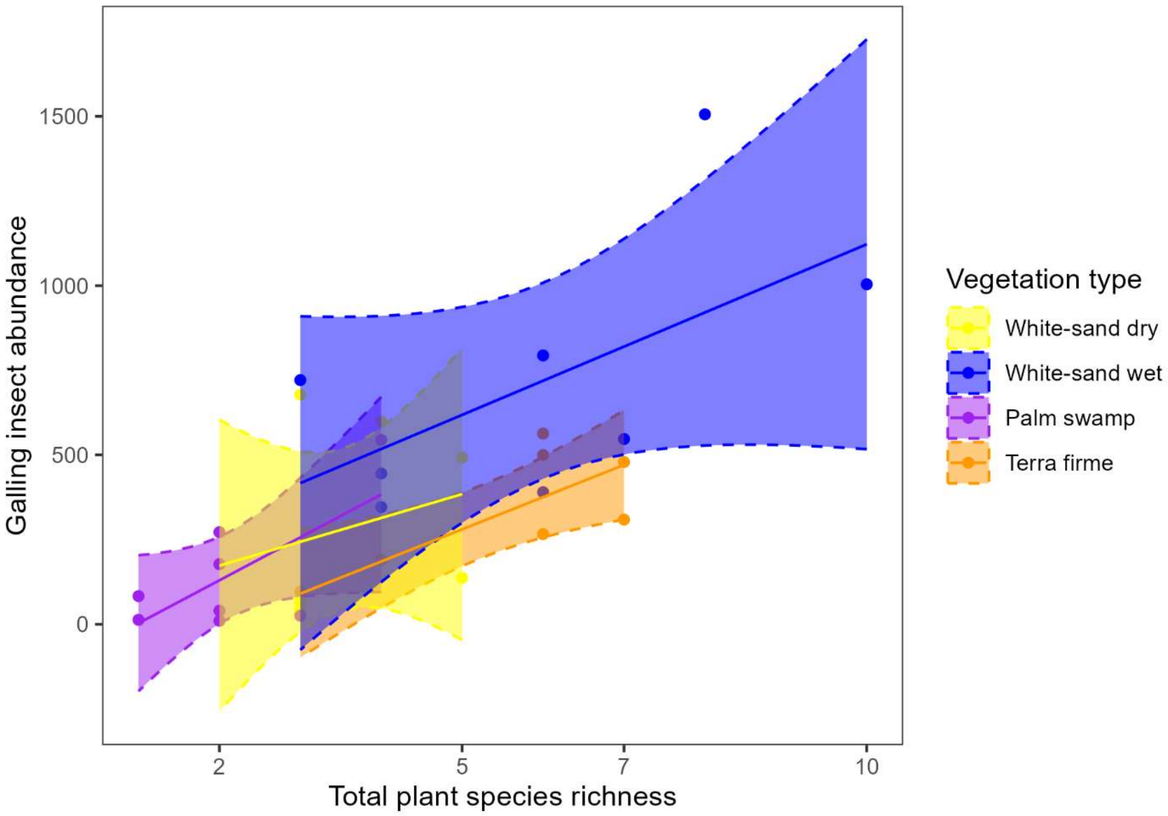

Figure 5 Relationship between galling insect abundance and total plant species richness in plots sampled in different vegetation types in the Peruvian Amazon. The dotted lines represent the model's 95% confidence intervals.

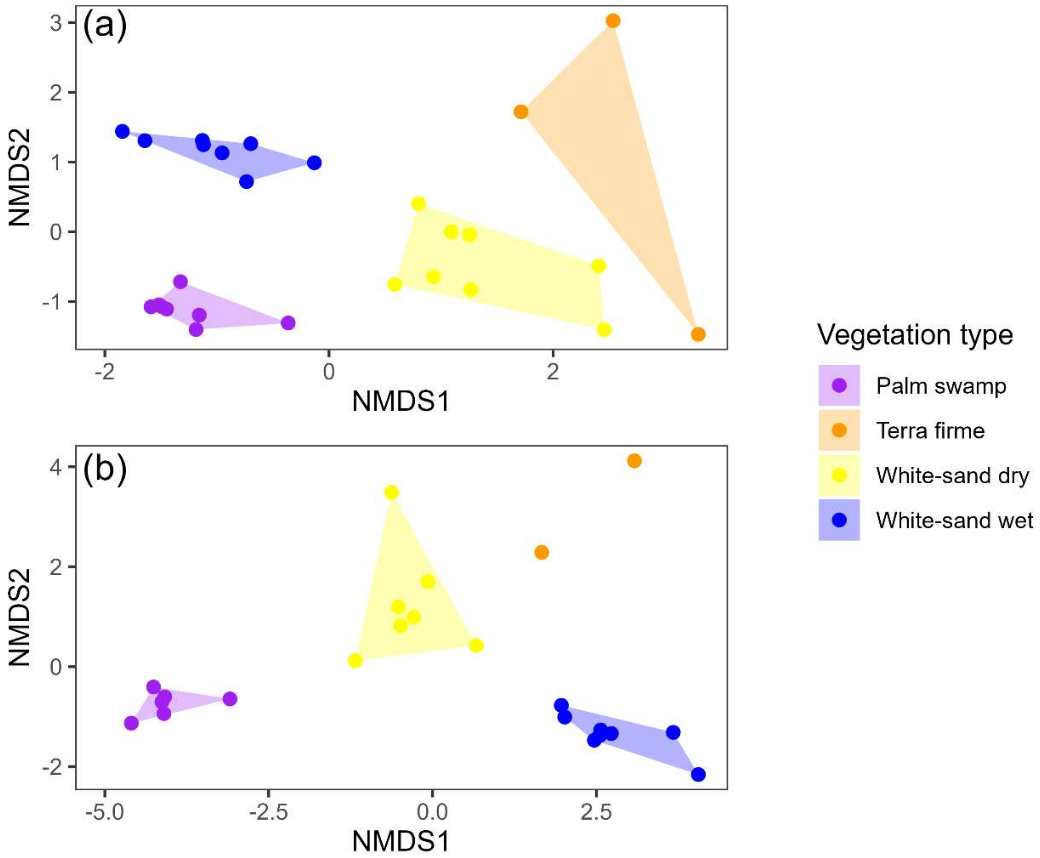

Figure 6 Non-metric multidimensional scaling (NMDS) plot showing the ordination of (a) plant species composition, and (b) galling insect composition between the vegetation types in the Peruvian Amazon.