

Global patterns of insect herbivory across forest canopies and understories: Insights from a tropical case study and a global comparison

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Abstract

Several studies have examined global patterns of insect herbivory, revealing variations with latitude, elevation, and temperature. However, less attention has been given to herbivory patterns at smaller spatial scales, particularly the comparison between forest canopies and understories. Understanding these finer-scale patterns is crucial for predicting ecological responses to both natural and anthropogenic changes. Differences in herbivory between the canopy and understory are expected due to distinct environmental conditions, with light availability being a key driving factor. To examine whether insect herbivory differs between the canopy and understory in different forest types, we estimated herbivory as leaf area loss [%] in the tree canopies and the woody understory of a montane dry – (MDF) and a montane rainforest (MRF) in southern Ecuador. For this, we collected around 20 leaves per plant of 918 plants in total in six 1 ha plots at two elevation levels (600 m, 1200 m) in the MDF and in nine 1 ha plots at three elevation levels (1000 m, 2000 m, 3000m) in the MRF. Additionally, we conducted a literature survey resulting in 64 studies used for the analyses to compare the herbivory pattern between the two strata in a multi-studies approach. Herbivory in the MDF

was – as expected – higher in the understory compared to the canopy. In the MRF, however, the pattern was reversed. The multi-studies approach revealed a mean herbivory of 9.45 % \pm 8.75 % (standard deviation) and no significant differences in herbivory between the canopy and the understory. Neither latitude as a proxy for temperature, nor precipitation, to account for different forest types, had significant effects on herbivory. Both the multi-studies and the MRF and MDF case study suggest that the variation in herbivory between forest types might be larger than between strata. However, for a better understanding of general herbivory patterns in the canopy and the understory of forest systems the need of much more case studies directly comparing both strata with each other is essential.

keywords: forest stratum, macro-ecology, community herbivory, light exposure, forest type

Introduction

Globally, herbivory in forests ranges between 7 % and 48 % (Coley & Barone, 1996; Metcalfe et al., 2014) and is mainly caused by insects (Coley & Barone, 1996). It is defined as the damage or loss of photosynthetic active tissue caused by the insect herbivore and is an important process influencing ecosystem functions such as nutrient cycles, water fluxes, and carbon sequestration (Hunter, 2001; Metcalfe et al., 2014; Prather et al., 2013; Schowalter et al., 1986). Insect herbivory affects the primary production and shapes the characteristics of plants along evolutionary time scales as well as the composition of plant assemblages along ecological time scales (Bagchi et al., 2014; Endara et al., 2015). In turn, various direct and indirect biotic and abiotic factors such as soil and climatic characteristics cause variations in insect herbivory across space and time (Liu et al., 2024). Studies have extensively explored these variations on large spatial scales, revealing that insect herbivory tends to increase toward lower latitudes and decrease with higher elevations (Galmán et al., 2018; Gao et al., 2019; Moles et al., 2011; Moreira et al., 2018). Furthermore, the herbivore incidence rate increases with rising temperatures (Kambach et al., 2016). Studying insect herbivory patterns at smaller spatial

scales, such as different forest strata, is crucial for understanding how herbivory varies within the same ecosystem, enabling more accurate predictions of ecological responses to natural and anthropogenic changes. However, little research has been done comparing insect herbivory between the canopy and the woody understory. (Heatwole et al., 2009; Maguire et al., 2016; Van Bael & Brawn, 2005; Zhang et al., 2023). Past research indicates that differences in insect herbivory across the vertical forest strata exist due to variable environmental conditions. One factor contributing to these different conditions is the variation in light availability along the vertical gradient of a forest, with the canopy being more sun-exposed and the understory more shaded (Valladares & Niinemets, 2008). Herbivory is influenced by light availability as it is higher in sun-exposed gaps within the understory compared to areas under the closed canopy (Piper et al., 2018). This might be due to specific leaf traits related to light exposure that affect herbivory (e.g., Coley & Barone, 1996; Cornelissen et al., 2003). Under sun-exposed conditions, leaves produce more secondary metabolites than under shaded conditions such as alkaloids, anthocyanins, and phenolic compounds (Coley & Barone, 1996; Karolewski et al., 2013; Koricheva et al., 1998; Ribeiro et al., 2011; Yang et al., 2018) which serve as plant defense substances and reduce herbivory (e.g., Coley et al., 1985; Gong et al., 2020; Moreira et al., 2017; Silva et al., 2012). Additionally, sun-exposed leaves tend to be smaller, thicker and have a lower specific leaf area (SLA) than shaded leaves which also tend to reduce herbivory (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2003; Werner & Homeier, 2015). Thus, we predict that leaves in the canopy are smaller, thicker, with lower SLA, and richer in secondary metabolites compared to leaves in the shaded understory (Valladares & Niinemets, 2008).

Forest structure, which is closely related to vertical light availability, is another factor that influences herbivory patterns within a forest. Forest structure is strongly shaped by climatic and topographical conditions as well as plant composition, resulting in different forest types

(Ehbrecht et al., 2021; Muscarella et al., 2020; Vanderwel et al., 2013). Therefore, annual precipitation can serve as a proxy for biomass production and therefore for forest structure (Lie et al., 2018). As an example, in tropical rainforests the high biomass production results in a homogeneous and closed canopy with little light reaching the understory. In contrast, tropical dry forests with a lower biomass production have more open and heterogeneous canopy covers, allowing more light to reach the understory layer (Brenes-Arguedas et al., 2011; Pan et al., 2013). Consequently, each forest creates unique conditions for its local herbivore communities (e.g., Brenes-Arguedas et al., 2011; Seifert et al., 2021). Nonetheless, the general pattern is a decrease in light availability from the canopy to the understory. Thus, we hypothesize that across forest types, canopies generally have higher concentrations of secondary metabolites and smaller and thicker leaves leading to lower herbivory compared to the understory (Lowman, 1985; Sérgio P. Ribeiro & Basset, 2016).

To examine this hypothesis, we first quantified insect herbivory in the canopy and the woody understory of two tropical forest types - montane rainforest (MRF) and montane dry forest (MDF) in southern Ecuador. Furthermore, to test the generality of our conclusions we contrasted our data with other studies around the world. For this, we extracted herbivory data from canopy- and understory layers from studies across the globe (excluding Antarctica).

Material and Methods

Study Area

The local study was conducted in a tropical montane rain- and dry forest of southern Ecuador. In the montane rainforest (MRF), we collected data at 1000 m, 2000 m, and 3000 m a.s.l. within the *Podocarpus National Park* (4°6' S, 78°5' W and 4°7' S, 79°10' W) and the *Reserva Biológica San Francisco* (3°58' S, 79°4' W) with an annual precipitation ranging from ≈1,800 mm y⁻¹ at 1000 m, 2,000 mm y⁻¹ at 2000 m to 2,500 mm y⁻¹ at 3000 m a.s.l. and a mean annual temperature decline from 19.9 °C at 1000 m, 14.6 °C at 2000 m, and 6.5 °C at 3000 m a.s.l.

(Limberger et al., 2021). In the montane dry forest (MDF), we collected data at 600 m and 1200 m a.s.l. within the *Laipuna Reserve* (4°12' S, 79°53' W) with a mean annual temperature of 24.1 °C and an annual precipitation of 249 mm (averaged across the years 2015, 2016, 2020, 2021, 2022) at 590 m a.s.l. (Bendix & Dobbermann, 2021). For the study, we established three 1 ha plots at each elevation in both systems resulting in 15 plots in total (nine in the MRF and six in the MDF).

Herbivory

To estimate arthropod herbivory in the canopies of the tree communities in both forest systems, we collected sun-exposed branches from 380 trees in the MRF belonging to 51 tree species in February and March 2019 and from 182 trees in the MDF belonging to 21 tree species in March and April 2022. For each tree, we randomly selected 20 mature leaves from the collected branches.

To estimate arthropod herbivory in the woody understory of the MRF and the MDF, we collected along two transects in each plot leaflets from 12 woody plants each plant of a volume of approximately 1 m³. Due to the huge workload, we decided to collect only leaflets instead of whole leaves. For simplicity, leaflets are named leaves in the following. Per plant, leaves were collected every 20 cm along a horizontal line at four different vertical levels, each 25 cm apart, resulting in 18 ± 2 leaves. Leaves were collected by randomly selecting the leaf closest to the respective measuring point. If no leaf was present, we collected the next leaf along a horizontal 90 ° angle from the measuring point to the center of the plant. If still no leaf was present, we omitted the collection of a leaf at that point. This way, we considered the density of the sampled plant. To account for temporal variation in the MDF during the rainy season, we did two sampling rounds in April and May 2022. For better comparability, we did also two collection rounds in the MRF in March and April 2023.

All collected canopy and understory leaves were scanned with a Canon scanner, CanoScan LiDE 120 (at 150 dpi pixel resolution). Scanned leaves were analyzed with the software WinFOLIA™ 2019a (Regent Instruments Inc., Quebec City, QC, Canada) to estimate first the original entire leaf area (as if there were no herbivory present) and then the herbivory as leaf area loss (LAL) in percent. LAL was defined as the loss of green leaf area comprising both missing- and dried as well as discolored leaf areas.

Literature survey

To gather data for the global comparison of herbivory between the two forest strata, we did a literature search in Web of Science on the 3rd and 11th of January 2024 by searching for the combinations of “insect herbivory” AND “forest” AND “canopy*”, “Insect herbivory” AND “forest” AND “understory*”, “insect*” AND “herbivory” AND “forest” AND “canopy*”, and “insect*” AND “herbivory” AND “forest” AND “understory*” in the abstracts or titles of scientific articles. In total, we got 551 hits of which we discarded studies dealing only with coniferous forests, seedlings, or herbaceous plants. Additionally, we did not include review articles, books, book chapters, studies with a modeling approach, studies dealing with herbivory caused by only one or a few herbivores, or studies describing herbivory experiments under artificial conditions with no control group. Apart from that, we included all articles dealing with foliar insect herbivory in the tree canopies or woody understory, including trees, shrubs, saplings, and sprouts, of forest ecosystems that were written in the English language.

From these 551 articles, we discarded 189 based on non-matching titles and 85 articles after reading the abstract. In addition, 171 articles were duplicates resulting in 106 articles. After careful reading of these studies, we excluded a further 42 articles resulting in 64 articles used for the final analyses. We extracted mean herbivory values in percent based on both continuous and categorical measurements. Values were either directly extracted from tables, calculated from corresponding datasets uploaded in repositories, or retrieved from figures with the web

tool WebPlotDigitizer (Rohatgi, 2022; Appendix Table S1). Median herbivory values of boxplots were used as mean values since we assumed an approximate normal distribution of the data in which the median and mean would be identical. Further, we noted whether the leaves on which herbivory was measured, were marked when starting to flush, to ensure to measure herbivory of a defined time period, or whether leaves were collected unmarked. In cases of species-level herbivory measurements, we added the respective phylogenetic information (genus, family, order) and noted whether the species was deciduous, semi-deciduous, or evergreen (plant functional type = PFT). To account for structural characteristics specific to different forest types influencing the vertical availability of light, we decided to use the mean annual precipitation. Precipitation was either noted in the papers or could be calculated from freely accessible worldwide high-resolution climate data. Thus, in cases of missing information on precipitation in the studies, we downloaded the monthly precipitation data of CHELSA (Karger et al., 2017, 2021) comprising values from the years 1979 to 2013 and calculated the average of the summed annual precipitation for each grid cell containing coordinates of our selected studies with missing precipitation data (for 25 out of 64 studies) with the packages *raster* and *sp* (Bivand et al., 2013; Hijmans, 2023; E. J. Pebesma & Bivand, 2005). Additionally, as a proxy for the annual mean air temperature, we calculated the absolute latitudinal distance of the study sites from the equator (De Frenne et al., 2013). To do this, we extracted the coordinates of the study locations or, in case of missing information, searched for the coordinates of described locations and converted them if needed into decimal degrees (WGS84) with the web tool online Coordinates Converter (<https://coordinates-converter.com>).

Statistical analyses

For the data collected in the MRF and the MDF in southern Ecuador, we fitted a generalized linear mixed model (GLMM) with a beta distribution with the package *glmmTMB* (Brooks et al., 2017) to analyze the significant effects of the predictor variables on herbivory. We used the relative mean herbivory as response and stratum nested within the forest type as well as the

scaled elevation as fixed effects. Although our primary focus was on the vertical comparison of herbivory between the canopy and understory, neglecting the impact of elevation would have overlooked a key variable that influences both plant and herbivore communities. Elevational gradients introduce variability that could interact with vertical stratification, making it essential to include elevation in our analysis. The plotID was added as a random effect. The results were plotted using the package *effects* (Fox & Weisberg, 2018, 2019).

To prepare the data of the global comparison of herbivory in forests between the two strata, we used the R packages *dplyr* (Wickham et al., 2020) and *tidyr* (Wickham, 2020). To visualize the distribution of the study sites within our dataset across the globe, we used the packages *sf* (Edzer Pebesma, 2018; Edzer Pebesma & Bivand, 2023) and *tmap* (Tennekes, 2018).

To examine the differences in mean herbivory [%] between the canopy- and the woody understory layer, we used three separate analyses: the first analysis was done on the plant species level including all studies describing herbivory on specific species. The second approach focused on the plant community level using only data from studies with measurements of community herbivory. The third approach contained only herbivory data from studies that compared both forest strata.

For the species-level analysis, we used the package *glmmTMB* (Brooks et al., 2017) to run a GLMM by using the relative mean herbivory as response variable and a beta-distribution as family function. As predictor variables we used the stratum as a factor, the absolute latitudinal distance of the study site from the equator, and the scaled annual precipitation. We included mean annual precipitation as a factor in our models, as it serves as a proxy for biomass production and forest structure variability. As control variables we added the PFT as factor and the factorial information of whether the leaves were marked or unmarked. To control for phylogeny, we included a nested random effect structure with species nested within genus, genus nested within family, and family nested within order. To account for the different

measurement techniques used in the studies, we included the study as a random effect. Additionally, to control for the robustness of each herbivory value, we weighed the values according to the relative number of measurements that were used to calculate the respective mean herbivory value compared to the summed number of repetitions of measurements across all studies.

To consider the plant community, we fitted a GLMM with the package *glmmTMB* (Brooks et al., 2017) containing the relative mean herbivory as response variable and a beta-distribution as family function. As predictor variables, we used again the stratum as a factor, the absolute latitudinal distance of the study site from the equator and the scaled annual precipitation. The study was added as random effect and the values were again weighed according to the relative number of measurements that were used to calculate the respective mean herbivory value.

For the third approach, we calculated the standardized mean difference in herbivory between the canopy and the understory (Hedges' *g*) for studies providing the mean, standard deviation (SD), and sample size for both strata, using the package *metafor* (Viechtbauer, 2010).

All statistical analyses were done with the software R version 4.3.1 (R Core Team, 2023) in RStudio version 2023.06.0 (Posit Team, 2023).

Results

In general, the herbivory was higher in the MRF compared to the MDF (Appendix Table S 2). The two forest strata canopy and woody understory showed forest-type specific patterns in the two forests of southern Ecuador. The MDF had higher mean herbivory values in the understory compared to the canopy (9.7 % \pm SD = 5.0 % compared to 7.4 % \pm 6.2 %), whereas the MRF had lower mean herbivory values in the understory compared to the canopy (5.4 % \pm 3.8 % compared to 13.5 % \pm 8.9 %; Appendix Table S2). The GLMM results underline forest-type-specific herbivory patterns with a significant increase in mean herbivory from the canopy to the

understory in the MDF and a significant decrease in mean herbivory from the canopy to the understory in the MRF (Table 1; Figure 1). The elevation had a positive effect on herbivory across both forest types indicating an increase of herbivory with increasing elevation (Table 1; Figure 1).

For the global comparison, we identified 64 studies published between 1991 and 2023 with 477 herbivory values [%] plus the corresponding information on the sample size from the searches in Web of Science to be appropriate for the multi-studies analysis. Hereof, 37 studies dealt with herbivory in tree canopies and 35 with herbivory in the understory. Eight studies, including the data of the case study described above, contained herbivory values from both the canopy and the understory. Hereof, five studies gave additional information on the sample size and the SD and were used for the analysis. Study areas were located in all continents except Antarctica (Figure 2) and comprised 159 plant species from 90 genera, 47 families, and 23 orders. Mean herbivory across all studies was $11 \% \pm SD = 9.2 \%$ in the understory and $8.1 \% \pm 7.9 \%$ in the canopy (Figure 3; Appendix Table S3).

For the species-level analysis, we could include 54 studies with 433 herbivory values [%]. Neither the stratum nor the precipitation had any significant effect on herbivory. All the remaining control variables had likewise no significant effect on herbivory (Table 2 a). The community-level analysis comprised 13 studies with 63 herbivory values [%]. There was again no significant effect on herbivory of either the stratum, the precipitation, or the absolute distance of the study site from the equator (Table 2 b). After calculating the standardized mean differences Hedges' g for the five studies containing herbivory data for both the canopy and the understory, we see inconsistent results: Hedges' g ranged from -0.64 to 0.50 (Figure 4).

Discussion

Our hypothesis of a lower herbivory in the sunny canopy compared to the shady understory due to light-dependent less palatable leaves in the canopy than the understory was not supported in

our case study from southern Ecuador. On the contrary, when not distinguishing between the forest types MRF and MDF, on average higher herbivory values in the canopy compared to the understory were observed (Appendix Table S2). However, when distinguishing between the forest types, we discovered forest type-specific patterns. The herbivory pattern in the MDF was in accordance with our assumption, but the herbivory pattern in the MRF showed the opposite pattern with lower herbivory values in the understory compared to the canopy. This was not expected based on our arguments of a light-driven vertical herbivory pattern detailed in the introduction and indicates that the stratum-specific differences in herbivory might be dependent on further specific characteristics of the forests. The MRF – unlike the MDF – had a dense and homogeneous canopy cover allowing less light to reach the ground compared to the MDF. This could have several not mutually exclusive implications. Firstly, the more shaded and thus less favorable conditions for plants in the understory compared to the canopy led to a relatively loose and patchy distribution of woody understory plants in the MRF (see also Liu et al., 2016). These plants were more apparent to herbivores than plants growing within dense vegetation. According to the apparency theory, more apparent plants are more often attacked by herbivores and thus produce more plant defense substances than less apparent plants (Martini et al., 2021; Strauss et al., 2015). As a consequence, the herbivory levels should decrease for apparent plants resulting in reduced herbivory levels in the understory of forests with a dense canopy cover and a loose understory vegetation. In addition, the abundance of insect herbivores decreases with decreasing leaf cover densities which can further decrease herbivory in a sparse understory (de Groot & Kogoj 2015). Secondly, the resource availability hypothesis supports the assumption of higher production of secondary metabolites in the understory, since it states that plants growing under low-light conditions (= low-resource availability) grow more slowly than under high-light conditions and invest more in defense to reduce their costs of compensative leaf production which follows after herbivory (Endara & Coley, 2011). Thirdly, the density of the foliar biomass was higher in the canopy compared to the understory forming large patches of

resources for herbivores. According to the resource concentration hypothesis, this could result in higher herbivore densities and consequently higher herbivory values in the canopy compared to the understory (Piper et al., 2018; Stephens & Myers, 2012). In support of a lower herbivore pressure in the understory, several studies found both lower herbivore densities and species richness in the understory compared to the canopy (Basset et al., 2001; Neves et al., 2014; Seibold et al., 2016).

The contradicting vertical herbivory pattern in the MDF compared to the MRF could be explained by forest-type-specific factors. One factor generally influencing the occurrence and structure of a forest is the precipitation and its seasonality (Murphy & Bowman, 2012; Wu et al., 2011; Zeppel et al., 2014). Thus, it can also affect the characteristics of the vertical strata and hence the vertical pattern of herbivory. Our statistical results suggested in general lower herbivory values in the MDF with a lower annual precipitation compared to the MRF which could give evidence of a relation to precipitation. Further, the precipitation in our study area increased with increasing elevation. Since the increasing elevation had a positive effect on herbivory in both forest types, this could be another evidence for the importance of precipitation on the vertical herbivory pattern. Additionally, the contradicting vertical herbivory pattern in the MDF compared to the MRF could partly be explained by the higher proportion of less palatable evergreen plant species in the canopy of the MDF compared to the understory layer with many better palatable deciduous plants as an adaptation to the strong seasonality. The less seasonal and wetter evergreen MRF in contrast contained many evergreen plants not only in the canopy but also in the understory. However, we should consider that the herbivory data in the MRF and the MDR and especially between the strata within the MRF were collected during different years. Thus, temporal variability in herbivory could also be the driver for our results.

To make general conclusions about the differences between forests and vertical strata, we performed a literature search. However, also our multi-study analysis showed neither a clear difference in herbivory between the two forest strata nor a clear pattern of differences in herbivory with environmental information like precipitation or temperature, two variables that are often related to herbivore communities as well as herbivory patterns (Ashton et al., 2011; Hodkinson, 2005; Piper et al., 2018; Weissflog et al., 2018). These observations could on the one hand be driven by methodological aspects, such as a mismatch of the scale of the modeled precipitation data from CHELSA and the study areas. These raster-based data can represent means of larger areas than the respective examined study area. Additionally, the annual precipitation does not reflect the seasonality which determines the forest structure (Staver et al., 2011). Concerning the latitude, which served as a proxy for the mean annual temperature, our results were in accordance with the meta-analysis results of Moles et al. (2011) demonstrating that there is no relation between latitude and herbivory. Nonetheless, the temperature pattern at local and regional scales is more complex than the simple latitudinal distance from the equator (e.g. due to topography) and might not be adequately represented by the latitude.

On the other hand, the observations could indicate that the variation of herbivory between different forest types might be larger than the variation between different strata within one forest. Gossner et al. (2014) even found differences in herbivory rates between spatially close-growing forests within the same climatic zone making abstractions of general herbivory rates on certain forest types and especially structures within forests challenging. Further, the understory conditions within a forest can change drastically in gaps produced by tree falls or other events (Richards & Coley, 2007). In these tree gaps, environmental conditions resemble the conditions in the canopy layer and herbivory rates tend to be higher in these sunny gaps compared to the shady understory (Piper et al., 2018). This gap-specific pattern can increase understory herbivory into similar levels of canopy herbivory. Additionally, the herbivory

pattern might depend on the age of a plant (juvenile or adult; Stiegel & Mantilla-Contreras, 2018) which, for trees, often is correlated with the stratum the leaves grow within a forest. With this in mind, studies could receive very different results when herbivory in the understory was measured either on evergreen and/or mature leaves of adult shrubs or on saplings since evergreen and mature leaves provide less palatable leaves than saplings with freshly flushing, young leaves (Coley & Barone, 1996; Coley, 1983; Ribeiro et al., 1994). Further, possible influences on the heterogeneity of herbivory in forests could be for instance the biomass productivity. Biomass productivity varies between forest types with higher biomass production in the MRF than in the MDF which can drive vertical differences in the forest structure (Muller-Landau et al., 2020). These differences in biomass production can cause changes in bottom-up and top-down forces on herbivory (Castagneyrol et al., 2017). In unproductive systems, predators are less likely to be present, so herbivore biomass increases as plant biomass increases. In more productive systems, predators control herbivores, so herbivore biomass is less responsive to increasing plant biomass. The forest cover, the forest fragment size, the urbanization gradient, the tree height, the tree diversity in general, or the phylogenetic distance to neighboring trees can be further factors influencing the heterogeneity of herbivory patterns in forests (Castagneyrol et al., 2014; Christie & Hochuli, 2005; Dodonov et al., 2016; García-Jain et al., 2022; Piper et al., 2018; Yguel et al., 2011; Zhang et al., 2023). All these patterns indicate a strong influence of the heterogenous environment on the vertical herbivory pattern. Finally, we have to consider that not only plants adapt to their environment but also insect herbivores. They can, for instance, be assigned to different feeding guilds, causing different damage types (e.g., Labandeira et al., 2007; Moran & Southwood, 1982) that show individual responses in herbivory between different strata (Gossner et al., 2014; Heatwole et al., 2009; Stiegel & Mantilla-Contreras, 2018). Additionally, insect herbivores constantly evolved counter-adaptations to the plant protection mechanisms (e.g., Awmack & Leather, 2002; War

et al., 2018). As a consequence, leaf traits might not be as important in shaping herbivory anymore as commonly assumed (Schön et al., 2024).

In addition, based on our search, we found only seven studies directly comparing herbivory in the canopy with the understory of which only four studies could be used for a meta-analysis in addition to our case study data. These five studies showed inconsistent patterns. Thus, for a decent and reliable analysis, we need further studies comparing herbivory in these two strata covering several forest types in various climatic zones to understand the forest type-specific mechanisms underlying vertical herbivory patterns. This knowledge is important for understanding the patterns and pressures of local herbivory on plants to maintain healthy forests capable of providing essential ecosystem services. It also helps to reveal the characteristics of herbivore communities and how both forests and herbivory may shift in response to changing environmental conditions.

Conclusion

In southern Ecuador, general herbivory was higher in the understory than the canopy in a montane dry forest, but lower in the understory than the canopy in a montane rainforest. This pattern contradicted our hypothesis of generally higher herbivory in the understory compared to the canopy. Furthermore, we found an increase in herbivory with increasing elevation. Comparing various studies across the globe describing herbivory patterns in the canopy or the understory revealed neither significant differences between these two strata nor significant correlations with the environmental factors precipitation, latitude as a proxy for temperature, and plant functional type. Comparisons between canopy and understory herbivory among the five studies dealing with both strata revealed again contradicting patterns, which indicates that the variation in herbivory between forest types might be larger than between strata. We conclude that understanding the variations of insect herbivory needs more detailed case studies that can be used in a real meta-analysis as well as within macro-ecological studies.

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Contributions

Jana E. Schön, Annemarie Wurz, Nina Farwig, and Roland Brandl designed the study. Jana E. Schön and Annemarie Wurz generated the herbivory data in the two southern Ecuadorian forest types. Jana E. Schön did the literature search for the multi-studies approach, collected the herbivory data, did all the analyses, and wrote the manuscript. All co-authors contributed to the development of the manuscript.

Conflict of Interest

The authors declare no conflicts of interest.

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Figures

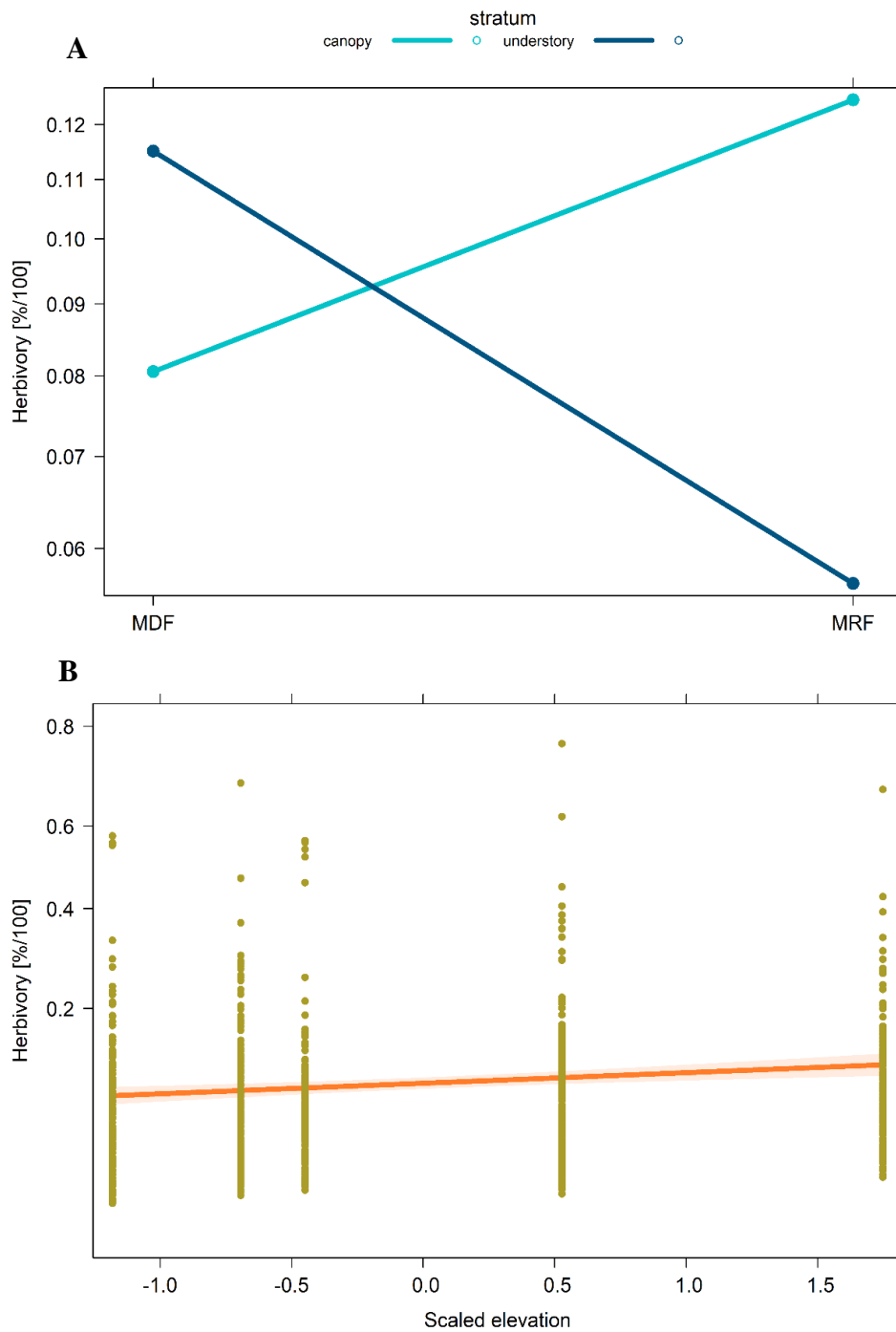


Figure 1 Significant influence of **A** the stratum per forest type on and **B** the scaled elevation [m a.s.l.] on the mean herbivory [%]. Plotted are the effects of the predictor variables against the partial residuals of the mean herbivory per plant. The orange lines represent the partial slopes of the effects, the blue line represents the loess smooth line of the partial residuals.

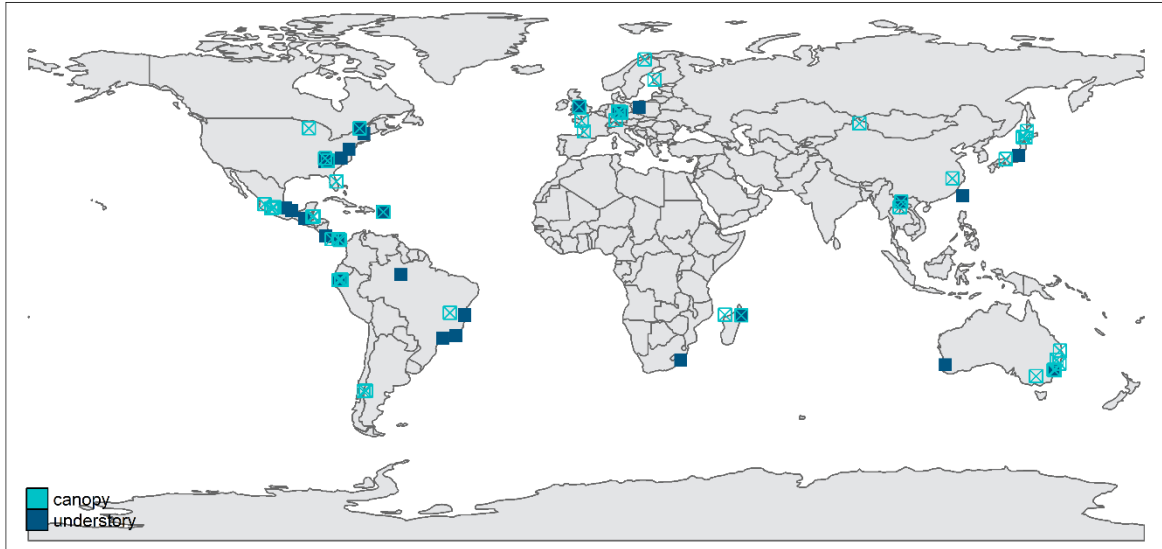


Figure 2 Distribution of the study sites examined in the 64 studies used in the multi-studies analysis. Light blue are studies examining herbivory in the canopy and dark blue in the understory.

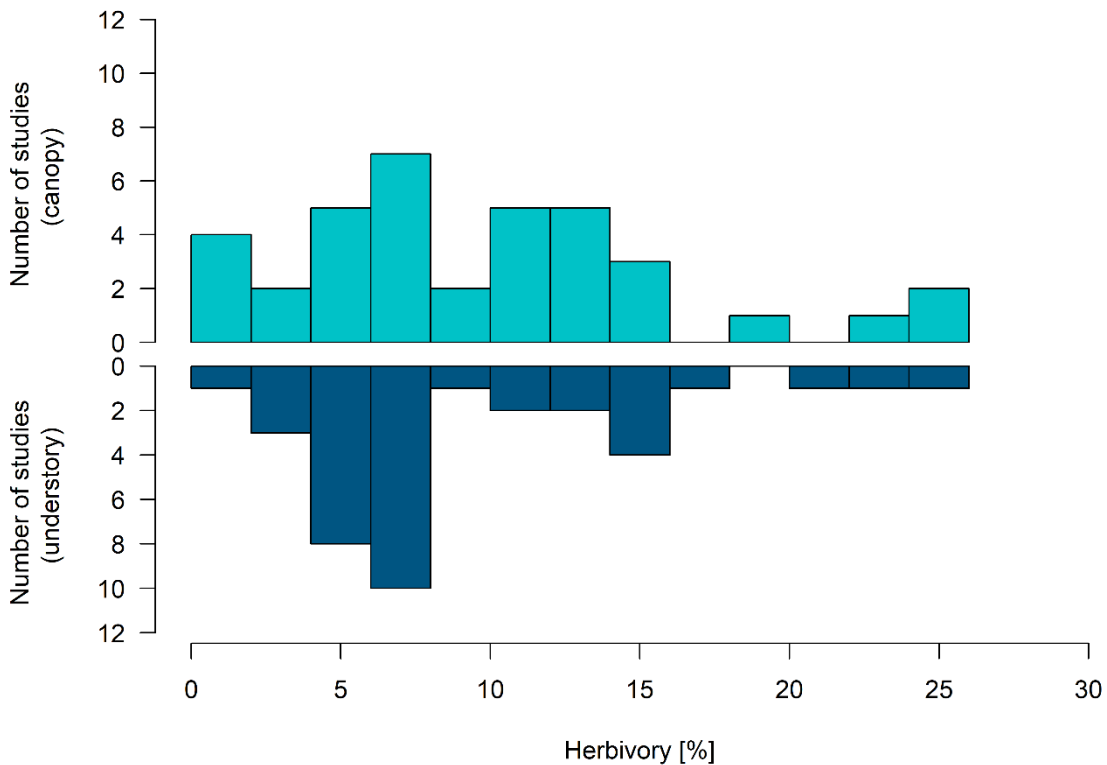


Figure 3 Number of studies of the multi-studies approach for specific mean herbivory values [%] for the canopy and the understory (n = 72).

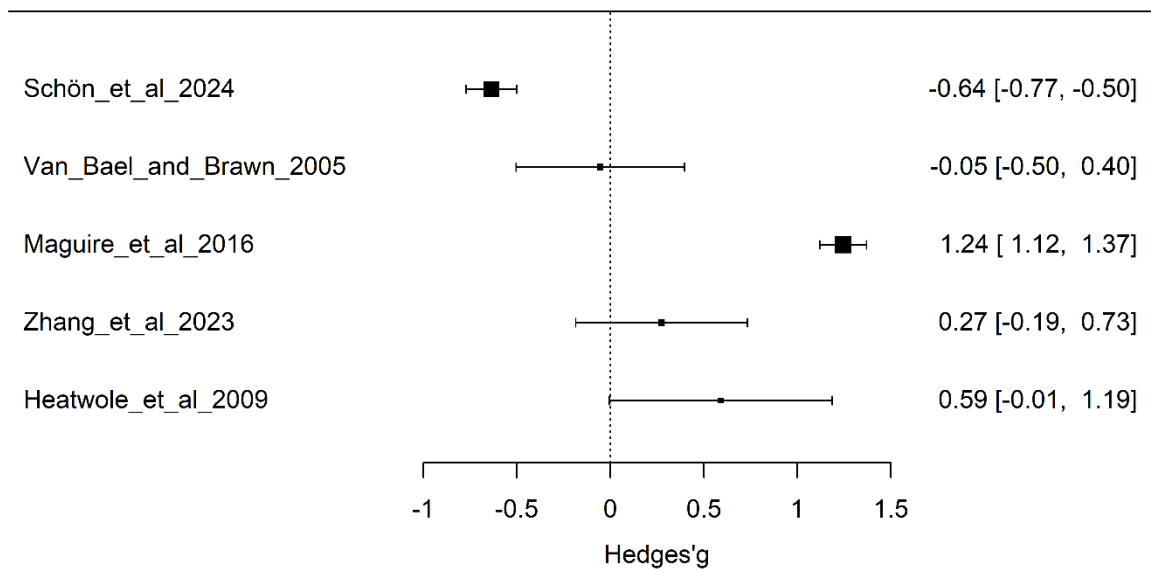


Figure 4 Forest plot showing the standardized mean differences Hedges'g in herbivory between the canopy and the woody understory for each study dealing with herbivory in both forest strata. Negative values indicate a higher herbivory in the canopy than the understory and positive values indicate a higher herbivory in the understory than the canopy. Numbers on the right represent the mean values and the lowest and highest variance in brackets.

Tables

Table 1 Results of the generalized linear mixed model including mean herbivory values of 918 plants growing in a montane dry forest (MDF) and a montane rainforest (MRF) in southern Ecuador. Significance was defined at a 5 % level.

Model	Fixed effects	Estimate	SE	p-value
Mean Herbivory [%]/100 ~ 1 + Forest type/Stratum + scale(Elevation) + (1 PlotID)	Intercept	-2.43	0.0586	< 0.001
	MRF	0.486	0.0699	< 0.001
	scale(Elevation)	0.104	0.0272	< 0.001
	MDF: understory	0.395	0.0754	< 0.001
	MRF: understory	-0.866	0.0612	< 0.001
	random effect	variance	SD	
	PlotID	3.51e ⁻¹⁰	1.87e ⁻⁰⁵	

Table 2 Results of the generalized linear mixed models including overall 64 studies with mean herbivory data on **a)** the species level comprising 53 studies (n = 414) and **b)** the community level comprising 13 studies (n = 63). Significance was defined at a 5 % level. Model results were weighed according to the relative number of plants used to calculate the corresponding mean herbivory value compared to the overall number of plants across all 53, respectively 13 analyzed studies. As model family, we used a beta-distribution. SE = standard error, stratum = factor: canopy or understory, Absl = absolute distance of the study site from the equator, marking = factor: previously marked or unmarked leaves to measure herbivory, PFT = plant functional type as factor: deciduous, semi-deciduous, evergreen, ID = unique number for each study, SD = standard deviation. Significance was defined at a 5% level.

Model	Fixed effects	Estimate	SE	p-value
a)				
Mean Herbivory [%]/100 ~ 1 + Stratum + Absl + scale(Precipitation) + Marking + PFT + (1 order/family/genus/species) + (1 ID)	Intercept	-1.4	4.76	0.768
	Understory	0.0553	2.34	0.981
	Absl	-0.0075	0.119	0.95

	Unmarked leaves	-0.72	2.45	0.769
	Scale(Precipitation):	-0.093	2.02	0.963
	PFT: evergreen	0.164	2.84	0.954
	PFT: semi-deciduous	0.132	9.9	0.989
	Random effects	Variance	SD	
	species:genus:family: order	3.14e ⁻¹¹	5.61e ⁻⁰⁶	
	genus:family:order	3.1e ⁻¹¹	5.57e ⁻⁰⁶	
	family:order	2.92e ⁻¹¹	5.4e ⁻⁰⁶	
	order	2.69e ⁻¹¹	5.19e ⁻⁰⁶	
	ID	2.74e ⁻¹¹	5.23e ⁻⁰⁶	
b)	Fixed effects	Estimate	SE	p-value
Mean Herbivory [%]/100 ~ 1 + Stratum + Absl + scale(Precipitation) + (1 ID)	Intercept	-2.28	0.904	0.0115
	Understory	-0.34	0.866	0.694
	Absl	-0.00127	0.0289	0.965
	Scale(Precipitation)	0.115	0.234	0.623
	random effects	variance	SD	
	ID	6.41e ⁻¹¹	8.01e ⁻⁰⁶	

1 Supplementary information

2 **Table S1:** Studies used for the global analysis to compare community herbivory [%] in the canopy- with the woody understory layer in forest
 3 ecosystems. PFT = plant functional type, c = canopy, u = understory, Marked = leaves were marked or unmarked before repeated herbivory
 4 measurements, m = marked leaves, unmarked leaves, N = number of replicates for mean herbivory measurements.

Study	Data source	Latitude	Precipitation [mm]	Stratum	PFT	Marked	N	Order	Family	Genus	Species
(Pérez-Solache et al., 2023)	Fig. 4f	19.3847953	899	c	deciduous	unm	90	Fagales	Fagaceae	Quercus	Q. castanea; Q. obtusata
(Nooten & Hughes, 2013)	Tab. 1	-33.8995	1150	u	evergreen	unm	120	Fabales; Myrtales; Proteales	Fabaceae; Myrtaceae; Proteaceae	Acacia; Daviesia; Angophora; Telopea	A. obtusata; D. corymbosa; A. hispida; T. speciosissima
(do Nascimento et al., 2019)	Fig. 1	-22.458333	2200	u	semi-deciduous; evergreen	unm	180	Sapindales; Laurales; Magnoliales	Sapindaceae; Siparunaceae; Annonaceae	Cupania; Siparuna; Xylopia	C. oblongifolia; S. guianensis; X. sericea
(Karolewski et al., 2013)	Tab 1	52.55	533	u	deciduous	unm	36	Dipsacales; Rosales; Cornales; Fagales	Adoxaceae; Rosaceae; Rhamnaceae; Cornaceae; Betulaceae	Sambucus; Prunus; Frangula; Cornus; Corylus	S. nigra; P. serotina; F. alnus; C. sanguinea; C. avellana
(Brezzi et al., 2017)	Text	29.214861	2000	c	NA	unm	510	community	community	community	community
(Nakamura et al., 2014)	Fig. 1	42.666667	1450	c	deciduous	unm	35	Fagales	Fagaceae	Quercus	Q. crispula
(Mazía et al., 2012)	Fig. 1	-40.583333; -40.716667	1533	c	deciduous	unm	300	Fagales	Nothofagaceae	Nothofagus	N. pumilio
(Schowalter & Ganio, 1999)		18.166667	3700	c	evergreen; NA	unm	264	Rosales; Malpighiales; Sapindales; Ericales; Arecales;	Urticaceae; Salicaceae; Burseraceae; Sapotaceae; Arecaceae;	Cecropia; Caesaria; Dacryodes; Manilkara; Prestoea;	NA

								Oxalidales	Elaeocarpaceae	Sloanea	
(Van Bael & Brawn, 2005)	Fig. 3	8.983333; 9.283333	2625	c/u	NA	unm	76	community	community	community	community
(Dyer et al., 2004)	Tab. 1	10.416667	4000	u	NA	unm	88	Piperales	Piperaceae	Piper	P. cenocladum
(Böhm et al., 2011)	Tab. 1	48.416667; 51.216667	822.7273	c	deciduous	unm	58	Fagales	Fagaceae	Quercus	Q. robur
(Vaca-Sánchez et al., 2023)	Tab. 5	20.79; 19.79; 19.67; 19.69; 19.44	1028.6	c	evergreen	unm	50	Fagales	Fagaceae	Quercus	Q. laurina
(Williams-Linera & Herrera, 2003)	Tab. 2	19.5; 19.533333	1610.1	u	evergreen	unm	360	Lamiales; Laurales; Gentianales; Myrtales;	Gesneriaceae; Lauraceae; Rubiaceae; Melastomataceae;	Moussonia; Ocotea; Palicourea; Miconia;	M. deppeana; O. psychotrioides; P. padifolia; M. glaberrima
(Maguire et al., 2016)	S3 Tab	45.67916769	830.5	c/u	deciduous	unm	560	Sapindales	Sapindaceae	Acer	A. saccharum
(Muiruri et al., 2015b)	(Muiruri et al., 2015a)	61.67222233	830.5	c	deciduous	unm	648	Fagales	Betulaceae	Betula	B. pendula
(Hamilton et al., 2004)	Fig. 1	35.966667	1160	u	deciduous; NA	unm	4536	Sapindales; Rosales; Saxifragales; Fabales; community	Sapindaceae; Ulmaceae; Altingiaceae; Fabaceae; community	Acer; Ulmus; Liquidambar; Cercis; community	A. rubrum; U. alata; L. styraciflua; Cercis canadensis; community
(Angulo-Sandoval et al., 2004)	Tab. 1	18.333333	1998	u	deciduous; evergreen	m	1920	Gentianales; Piperales; Malpighiales; Sapindales; Ericales; Oxalidales; Lamiales	Rubiaceae; Piperaceae; Salicaceae; Burseraceae; Meliaceae; Sapotaceae; Elaeocarpaceae; Bignoniaceae	Palicourea; Piper; Salicaceae; Dacryodes; Guarea; Manilkara; Sloanea; Tabebuia	P. riparia; P. glabrescens; C. arborea; D. excheha; G. guidonia; M. bidentata; S. berteriana; T. heterophylla
(Neves et al., 2010)	Fig. 2A	-15.60075	975	c	NA	unm	30	community	community	community	community
(Stiegel et al., 2017)	Fig. 4a, b	51.320314	674	c/u	deciduous	unm	128	Fagales;	Fagaceae; Betulaceae;	Fagus; Carpinus;	F. sylvatica; C. betulus;

								Sapindales	Sapindaceae	Acer	<i>A. pseudoplatanus</i>
(Christie & Hochuli, 2005)	Fig 2	-33.85217	960	c	evergreen	unm	25	Myrtales	Myrtaceae	Angophora	<i>A. costata</i>
(Schowalter, 1994)	Fig. 2	18.166667	3720	c	evergreen; deciduous	unm	109	Malpighiales; Rosales; Sapindales; Ericales; Oxalidales	Salicaceae; Urticaceae; Burseraceae; Sapotaceae; Elaeocarpaceae	Casearia; Cecropia; Dacryodes; Manilkara; Sloanea	<i>C. arborea</i> ; <i>C. peltate</i> ; <i>D. excelsa</i> ; <i>M. bidentate</i> ; <i>S. berteriana</i>
(Oliveira et al., 2012)	Fig. 3	-14.879861	871	c	deciduous	m	120	Lamiales	Bignoniaceae	Handroanthus	<i>H. spongiosus</i>
(Nakamura et al., 2021)	S Fig. 1	42.816667	1149	c	deciduous	unm	30	Fagales	Betulaceae	Betula	<i>B. ermanii</i>
(García-Jain et al., 2022)	Fig. 1	19.79165	1024	c	semi- deciduous	unm	90	Fagales	Fagaceae	Quercus	<i>Q. deserticola</i>
(Gossner, Pašalić, et al., 2014)	Fig. 1	50.8675	683	c/u	deciduous	unm	925	Fagales	Fagaceae	Fagus	<i>F. sylvatica</i>
(Kristensen et al., 2020)	Fig. 2a	68.35	865.5	c	deciduous	unm	189	Fagales	Betulaceae	Betula	<i>B. pubescens</i>
(Lee et al., 2021)	Fig. 2	42.666667	1269	c	deciduous	unm	100	Fagales	Fagaceae	Alnus	<i>A. hirsuta</i>
(Shure et al., 1998)	Tab. 5	35.9	1400	c	deciduous	unm	189	Fagales; Sapindales	Fagaceae; Sapindaceae	Quercus; Acer	<i>Q. alba</i> ; <i>Q. prinus</i> ; <i>A. rubrum</i>
(Fowler, 1993)	Fig. 4	-2.4	2690	u	evergreen; NA	unm	402	Boraginales; Gentianales; Malpighiales; Myrtales; Fabales	Boraginaceae; Rubiaceae; Chrysobalanaceae; Melastomataceae; Caesalpinaceae	Cordia; Duroia; Hirtella; Maieta; Tococa; Tachigalia	<i>C. nodosa</i> ; <i>Duroia</i> sp.; <i>H. physophora</i> ; <i>M. guianensis</i> ; <i>Tococa</i> sp.; <i>T. myrmecophila</i>
(Feller & Chamberlain, 2007)	Tab. 2	16.83	3005	c	evergreen	unm	486	Malpighiales	Rhizophoraceae	Rhizophora	<i>R. mangle</i>
(Gherlenda et al., 2016)	Tab. 1	-33.616667	876	c	evergreen	m	99	Myrtales	Myrtaceae	Eucalyptus	<i>Eucalyptus tereticornis</i>
(Shure & Wilson, 1993)	Fig. 6	35.183583	187.5	u	deciduous	unm	120	Fabales; Cornales; Magnoliales; Sapindales	Fabaceae; Cornaceae; Magnoliaceae; Sapindaceae	Robinia; Cornus; Liriodendron; Acer	<i>R. pseudoacacia</i> ; <i>C. florida</i> ; <i>L. tulipifera</i> ; <i>A. rubrum</i>

(Feller, 2002)	Fig. 1B	16.83	3005	c	evergreen	unm	50	Malpighiales	Rhizophoraceae	Rhizophora	R. mangle
(Zhang et al., 2023b)	(Zhang et al., 2023a)	21.616667	1493	c/u	NA	unm	234	community	community	community	community
(Yves Basset, 1991)	Fig. 1A	-27.322222	1285	c	evergreen	unm	40	Malvales	Malvaceae	Argyrodendron	A. actinophyllum
(Binli Wang et al., 2022)	Fig. 3	47.309034	138	c	deciduous	unm	150	Malpighiales	Salicaceae	Populus	P. laurifolia
(Roberts et al., 2022)	Fig. 2	52.801	762	c/u	deciduous	unm	756	Rosales; Fagales; Sapindales	Rosaceae; Betulaceae; Fagaceae; Sapindaceae	Crataegus; Corylus; Quercus; Acer	C. monogyna; C. avellana; Q. robur; A. pseudoplatanus
(Heatwole et al., 2009)	Fig. 2	-15.73	2415	c/u	NA	unm	48	community	community	community	community
(Radho-Toly et al., 2001)	Tab. 2	-31.962161	869	u	evergreen	m	40	Myrtales	Myrtaceae	Eucalyptus	E. cladocalyx; E. botryoides; E. marginata; E. gomphocephala
(Feller et al., 2013)	Fig. 2A	28.240709; 16.83; 9.304091	2331.13	c	evergreen	unm	54	Malpighiales	Rhizophoraceae	Rhizophora	R. mangle
(Stone & Bacon, 1995)	Tab. 1	-35.75	381	c	evergreen	m	84	Myrtales	Myrtaceae	Eucalyptus	E. camaldulensis
(Dodonov et al., 2016)	Fig. 2	-15.466667	2000	u	NA	unm	200	Gentianales	Rubiaceae	NA	NA
(Stephan et al., 2017)	Fig. 3b	36.774053	2277	u	evergreen	unm	120	community	community	community	community
(Yguel et al., 2011)	Text	48.193099	814	c	NA	unm	40	Fagales	Fagaceae	Quercus	Q. sp.
(Morante-Filho et al., 2016)	Text	-15.833333	2000	u	NA	unm	120	community	community	community	community
(Chelse Prather, 2014)	Fig. 2, 3	18.316667	2635	u	evergreen	m	286	Malpighiales; Ericales; Oxalidales; Myrtales; Apiales	Salicaceae; Sapotaceae; Elaeocarpaceae; Melastomataceae; Araliaceae	Casearia; Manilkara; Sloanea; Miconia; Schefflera	C. arborea; M. bidentate; S. berteriana; M. prasina; M. racemosa; S. morototoni

(Lind et al., 2012)	Fig. 3	38.886	1024	u	deciduous	unm	50	Lurales	Lauraceae	Lindera	L. benzoin
(Massad, et al., 2022)	(Massad, et al., 2022)	-23.2936	1594	u	evergreen; NA	unm	1338	Piperales	Piperaceae	Piper	P. gaudichaudianum; P. lhotzkyanum; P. cubataonum; P. hispidum; P. pilosa; P. hillianum; P. translucens; P. solmsianum; P. corintoanum; P. truncatum; P. cernuum; P. richardiifolium; P. caudensis; P. malacophyllum; P. schenckii; P. 1974; P. 1975; P. arboreum; P. lepturum; P. dilatatum; P. acute; P. elongate; P. ovalelongate; P. asymmetrical; P. biground; P. cordate; P. evenbase; P. hermmendorfii; P. overlapping; P. biglf
(Adams & Fiedler, 2016)	Fig. 2g	-3.971667	2200	u	evergreen; deciduous	unm	150	Sapindales; Lamiales; Malvales	Meliaceae; Bignoniaceae; Malvaceae	Cedrela; Handroanthus; Heliocarpus	C. montana; H. chrysanthus; H. americanus
(Fonseca, 1994)	Tab. 2a	-2.4	2186	u	evergreen	m	40	Fabales	Fabaceae	Tachigali	T. myrmecophila

(Farnsworth & Ellison, 1991)	Tab. 1	16.586927	2461	c	evergreen	unm	120	Malpighiales	Rhizophoraceae	Rhizophora	R. mangle
(Reynolds & Crossley, 1997)	Tab. 1	35.060251	1476	c	deciduous	unm	44	Sapindales; Fagales	Sapindaceae; Fagaceae	Acer; Quercus	A. rubrum; Q. rubra
(Tanaka & Nakamura, 2015)	Fig. 5a	44.79	1225	c	deciduous	unm	20	Malpighiales	Salicaceae	Salix	S. udensis
(Valdés-Correcher et al., 2020)	Text	44.68	929	c	deciduous	unm	470	Fagales	Fagaceae	Quercus	Q. robur
(Christie & York, 2009)	Fig. 1	-31.55	1585	c	evergreen	unm	180	Myrtales	Myrtaceae	Eucalyptus	E. pilularis
(Strong et al., 2000)	Fig. 3	43.93942	938	u	deciduous	unm	42	Sapindales	Sapindaceae	Acer	A. saccharum
(Dudt & Shure, 1994)	Fig. 6	34.685979	1400	u	deciduous	unm	1440	Magnoliales; Cornales	Magnoliaceae; Cornaceae	Liriodendron; Cornus	L. tulipifera; C. florida
(Ruiz-Guerra et al., 2010)	Fig. 2a	18.583333	4900	u	NA	unm	1054	community	community	community	community
(Martini et al., 2022)	Fig. 1c	23.575	2929	u	evergreen	unm	74	Fagales; Ericales; Laurales	Fagaceae; Pentaphylacaceae; Lauraceae	Castanopsis; Eurya; Litsea; Machilus	C. fabri; E. loquaiana; L. acuminata; M. thunbergii
(Botzat et al., 2013)	Fig. 3b	- 30.49583325	920	u	NA	unm	240	community	community	community	community
(Fáveri et al., 2008)	Fig. 2	-2.416667	2700	u	NA	unm	1100	community	community	community	community
(Boege et al., 2011)	Text	16.1329	3850	u	evergreen	unm	65	Fabales	Fabaceae	Dialium	D. guianense
(Aide, 1993)	Tab. 1	9.15	2566	u	evergreen; NA	m	7680	Malpighiales; Gentianales;	Euphorbiaceae; Chrysobalanaceae; Violaceae; Lacistemataceae; Ochnaceae; Clusiaceae; Rubiaceae;	Acalypha; Hirtella; Hybanthus; Rinorea; Lacistema; Ouratea; Garcinia; Alseis; Coussarea; Famea;	A. diversifolia; H. triandra; H. prunifolius; R. sylvatica; L. aggregatum; O. lucens; G.intermedia; A. blackiana; C. curvigemma; F. occidentalis;

								<p>Lurales; Brassicales; Magnoliales;</p> <p>Myrtales;</p> <p>Sapindales;</p> <p>Rosales;</p> <p>Ericales; Piperales; Fabales;</p> <p>Malvales;</p>	<p>Lauraceae; Capparaceae; Annonaceae; Myristicaceae; Myrtaceae; Melastomataceae; Meliaceae;</p> <p>Burseraceae;</p> <p>Sapindaceae;</p> <p>Moraceae;</p> <p>Sapotaceae; Piperaceae; Fabaceae;</p> <p>Malvaceae;</p>	<p>Psychotria; Beilschmiedia; Capparis; Desmopsis; Virola; Eugenia; Mouriri; Guarea;</p> <p>Trichilia; Protium;</p> <p>Talisia; Tetragastris; Poulsenia; Sorocea; Pouteria; Piper; Prioria; Swartzia; Tachigali; Quararibea;</p>	<p>P. horizontalis; B. péndula; C. frondosa; D. panamensis; V. sebifera; E. oerstedeana; M. myrtilloides; G. guidonia; G. sp.; T. tuberculata; P. panamense; P. tenuifolium; T. princeps; T. panamensis; P. armata; S. affinis; P. unilocularis; P. cordulatum; P. copaifera; S. simplex; T. versicolor; Q. asterolepis;</p>
Schön, et al. (in prep)	Tab	-4.115857 -3.966667 -4.116833 -4.115857 -3.966667 -4.116833 -4.210064 -4.228425 -4.210064 -4.228425	1540.6	c/u	NA	unm	916	community	community	community	community

6 **Table S2** Case study measures for the local herbivory estimations (n = 918) from southern Ecuador in the montane dry forest (MDF) and the montane
 7 rainforest (MRF). SD = standard deviation, canopy n = 562, understory n = 356.

Class	Minimum [%]	Mean [%]	SD [%]	Maximum [%]
Overall	0.18	9.8	7.68	59.44
MDF	0.36	8.43	5.79	35.24
MRF	0.18	10.54	8.44	59.44
Understory	0.18	7.08	4.78	35.24
Canopy	0.36	11.52	8.62	59.44
MDF:understory	2.02	9.74	4.97	35.24
MDF:canopy	0.36	7.43	6.18	32.13
MRF:understory	0.18	5.36	3.77	21.94
MRF:canopy	0.62	13.48	8.94	59.44

8

9 **Table S3** Information on the general mean herbivory and specifically on herbivory in the canopy and the understory across all plants within the 64
 10 analyzed studies (canopy n = 219, understory n = 258. SD = standard deviation.

Measure	Canopy	Understory	Overall
Minimum	0.02	0.006	0.006
Mean	8.09	10.61	9.45
Maximum	54.95	61.00	61.00
SD	7.94	9.24	8.75

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