Herbivory in the Malaysia Rain Forest Canopy, Penang Hill

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Abstract

As part of the international "Expert Bio Blitz" on Penang Hill in October of 2017, a team of scientists and citizen scientists collected information on the amount of herbivory from insect defoliators in the predominant canopy tree species. Professional tree climbers associated with the Bio Blitz collected leaf samples, and herbivory was measured on replicate leaves from the harvested samples. Defoliation (expressed as percentage of the leaf area loss) showed a range from 0% in *Ficus sp.* to 61.9% in one individual tree of *Cinnamomum porrectum*. These observations were compared against a larger database of leaf samples (also measured by citizen scientists) from the Amazon rain forest canopies of Peru earlier in the year, and in the future, this will be integrated into a global database representing ten tropical rain forest regions. In addition to providing a rapid assessment of the insect damage to the forest canopy on Penang Hill, the data collection created an educational outreach experience whereby international high school students teamed up with expert scientists and contributed their efforts. The herbivory survey on Penang Hill achieved two major goals: scientific information about the biodiversity and canopy processes on Penang Hill, and an important educational outreach experience for a team of international students, including a predominance of girls.

Introduction

The resource availability of green foliage for herbivores in forests appears enormous, particularly in primary tropical rain forests, with their tall trees and multi-layered canopies. But, while clearly different tree species vary in the quality of resources for herbivores and in their subsequent herbivory rates (e.g. Coley 1982, Lowman 1985, Lowman and Rinker 2004), the variability in both availability and utilization of green foliage both within and among canopies of different rain forest trees has not been well quantified (but see Lowman, Devy and Ganesh 2014). The majority of earlier studies of herbivory in rain forests involved discrete harvests of lower canopy leaf samples (or even worse, selection of leaves on the forest floor) and simple measurements of leaf surface area missing, a simplistic approach to a complex interaction (e.g. Odum and Ruiz-Reyes 1970, Hairston et al 1960). This type of approach obviously does not account for leaves totally eaten by herbivores and does not provide an objective spatial assessment since the canopy leaves are not part of most sampling techniques. The variability of biological and environmental conditions throughout the complex vertical distribution of rain forest foliage affects leaf palatability (Lowman and Box 1983). Important factors include light, height, aspect of canopy region, age of leaves, species of trees, elevation, and other spatial and temporal factors (see Lowman 1985). In addition to affecting leaf chemistry and structure, some of these factors (e.g. light, species, height) may also act as constraints to the distribution of herbivores.

Herbivory in Australian rain forests was predominantly carried out by insects, with a very small proportion of leaf area losses to birds or mammals (Lowman and Schowalter 2012). A similar result was the case in Amazonian rain forest canopies (Lowman 2014), but with a very small number of canopy tree species consumed by sloths (Voirin et al 2013). A long-term survey of herbivore biodiversity in Penang rain forest canopies has not been conducted (but see earlier review in Montgomery 1975), although it is likely that insects also represent the predominant herbivore group throughout tropical rain forest canopies of the world, as is the case elsewhere. Although the leaves in this survey were discrete collections (or snapshots) of one point in time, the collections were made from the canopy and were carefully quantified with respect to important spatial and temporal factors (see Lowman 1984). The application of R in herbivory measurements was implemented for our long-term leaf database in earlier studies as a pilot (Kaganovskiy and Lowman 2012) but is expanded here as a useful tool for canopy data analysis.

Whereas biodiversity surveys (also known as bio blitzes or expert bio blitzes) are rapid assessments to document species diversity (Parker et al 2018), additional information about the interactions of existing biodiversity is equally important in terms of defining a forest ecosystem and assessing forest health. In Penang, our expert bio blitz involved over 100 scientists surveying the majority of taxa from the forest floor to the treetops. This information will contribute to the UNESCO world heritage Man and the Biosphere nomination of this rain forest site. However, thanks to a team of high school citizen scientists, additional information on the interactions of insect herbivores and canopy trees was also collected. These data provide a quick snapshot of the insect pressure on canopy trees at Penang Hill and will subsequently be compared against a global database of several hundred such canopy trees amassed through citizen science efforts over twenty-five years (Lowman, unpublished data).

Methods

Using a protocol developed in the Amazon approximately two decades ago, information about leaf areas and proportions consumed by herbivores were quantified during the Penang Hill bio blitz, October 2017. This protocol (affectionately called the Lowman Leaf Lovers Club, see www.canopymeg.com) has amassed several thousand leaves in a global database over the years that all reflect a discrete snapshot of herbivory for one defined population of leaves at one point in time. It was first developed for Australian rain forests (Lowman 1984) and has been applied to

Madagascar (Heatwole et al 2009), old growth conifer forests in the Pacific Northwest (Ernest et al 2006, Shaw et al 2006), and many other tropical rain forests (reviewed in Lowman and Rinker 2004a). This method has obvious limitations, because it tends to underestimate herbivory, since leaves entirely consumed are not visible in the discrete (or snapshot) samples. But it has the benefit of providing a rapid assessment of potential insect outbreaks, with relative comparisons within and between species and canopy levels. Extensive information about the pros and cons of herbivory methodology are available elsewhere (Lowman 1984, 1997).

In the case of this survey, dedicated climbers collected samples of 30 leaves from the major canopy tree species on Penang Hill with respect to specific spatial and temporal variables (Figure 1).

Figure 1. Canopy access team collected leaves as well as other treetop samples.

In a few cases, 30 leaves were not available to the climbers, since each sample required leaves of the same height, age and light levels. Each leaf sample was measured for length, width, potential leaf area (PLA, meaning area of each leaf before herbivores attacked), and actual leaf area (ALA, the remaining photosynthetic surface area of the leaf after insect attack). The PLA and ALA were accurately measured using graph paper, since there was not reliable access to electricity or ability to bring an electronic digitizer or scanner to this remote forest site (Figure 2). In addition, the citizen science team eye-estimated the amount of leaf mining on each leaf, which is where brown areas indicate that an herbivore either burrowed through one of the leaf layers, or leaf-sucking herbivores created brown spots on the leaf surface. Over 20 high school students assisted with this leaf measurement activity, giving them first-hand field experience working with canopy foliage in a tropical rain forest. The team approach also reduced any personal bias with regard to the measurement techniques.

Figure 2. Students measuring leaves to survey herbivory from the Penang Hill forest canopy.

Data were analyzed using R, Tableau and subsequent analyses of variance performed (ANOVA) to compare aspects of the data with respect to certain spatial and temporal factors.

Results and Discussion

Penang herbivory and mining were assessed for each genus, and where possible, species identification as well (Table 1).

Table 1: Statistical summary of percentages eaten and mined by genus and species in Penang.

Genus	Species	Number of Records	Avg. Height (Meters)	Avg. Percent Eaten	Avg. Percent Mined	Eaten SE	Mined SE
Agathis	borneensis	60	17.50	1.11	3.53	0.40	0.70
Campnosperma	auriculatum	25	22.60	24.95	0.00	2.20	0.00
Cinnamomum	porrectum	50	23.00	31.09	3.00	3.75	0.40
Ficus	sp.	20	22.00	0.00	0.00	0.00	0.00
Garcinia	sp.	60	25.00	2.88	0.58	1.15	0.20
Schima	wallichii	30	19.00	11.83	0.00	2.20	0.00
Shorea	bracteolata	30	40.00	10.13	0.00	2.10	0.00

The herbivory (i.e. holes consumed in leaf surfaces) ranged from 0% leaf area eaten (Ficus sp.) to 61.9% defoliation in one individual of *Cinnamomum porrectum*, as shown in Table 1 as well. This data set from the Penang canopy represents the first time, after sampling hundreds of trees for snapshot herbivory as in this survey, that any set of leaves had absolutely no herbivory (ML, personal comm.).

The graphical representation of the averages by genus with standard errors is shown in Figure . In contrast, mining (i.e. surface damage) ranged from negligible for the genera *Shorea*, *Schima* and *Campnosperma*, to only 3.5% for *Agathis* (as shown in Figure).

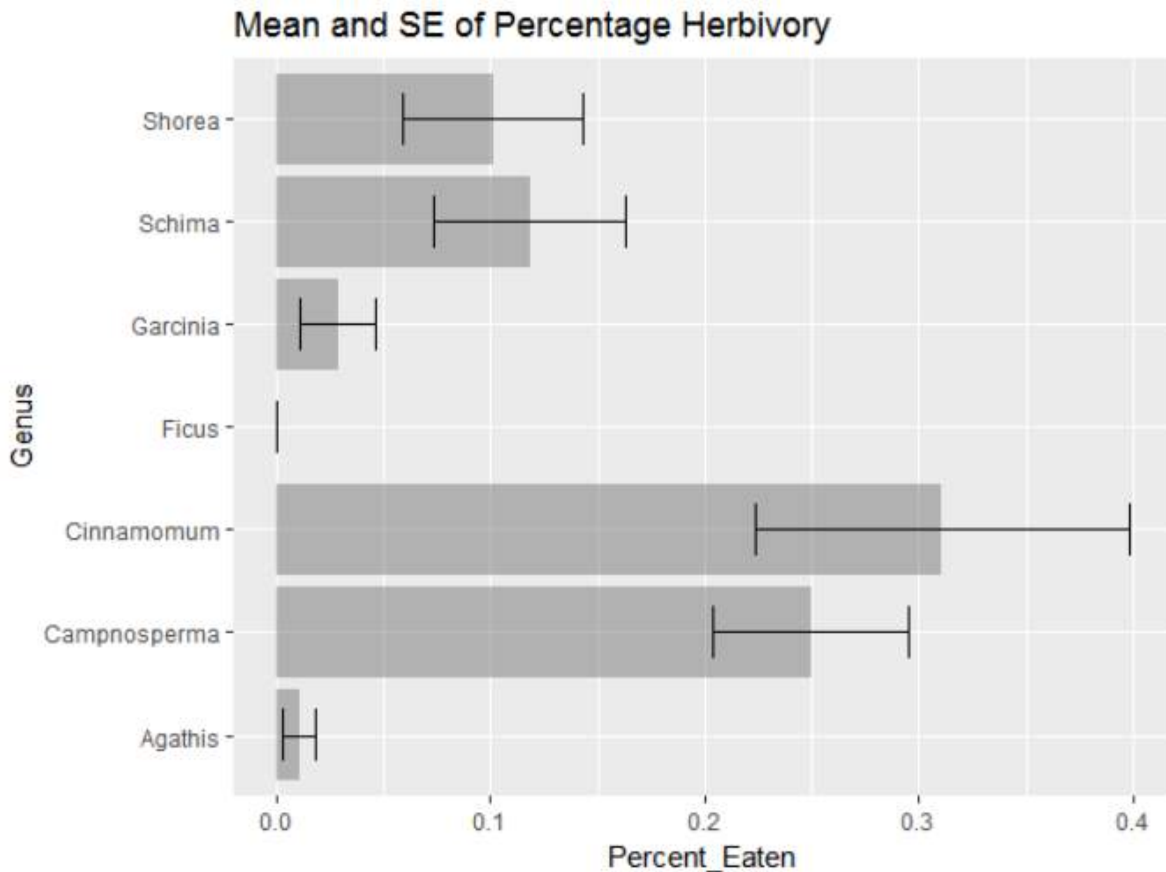

Figure 3. Mean percentage eaten by genus (with Standard Errors).

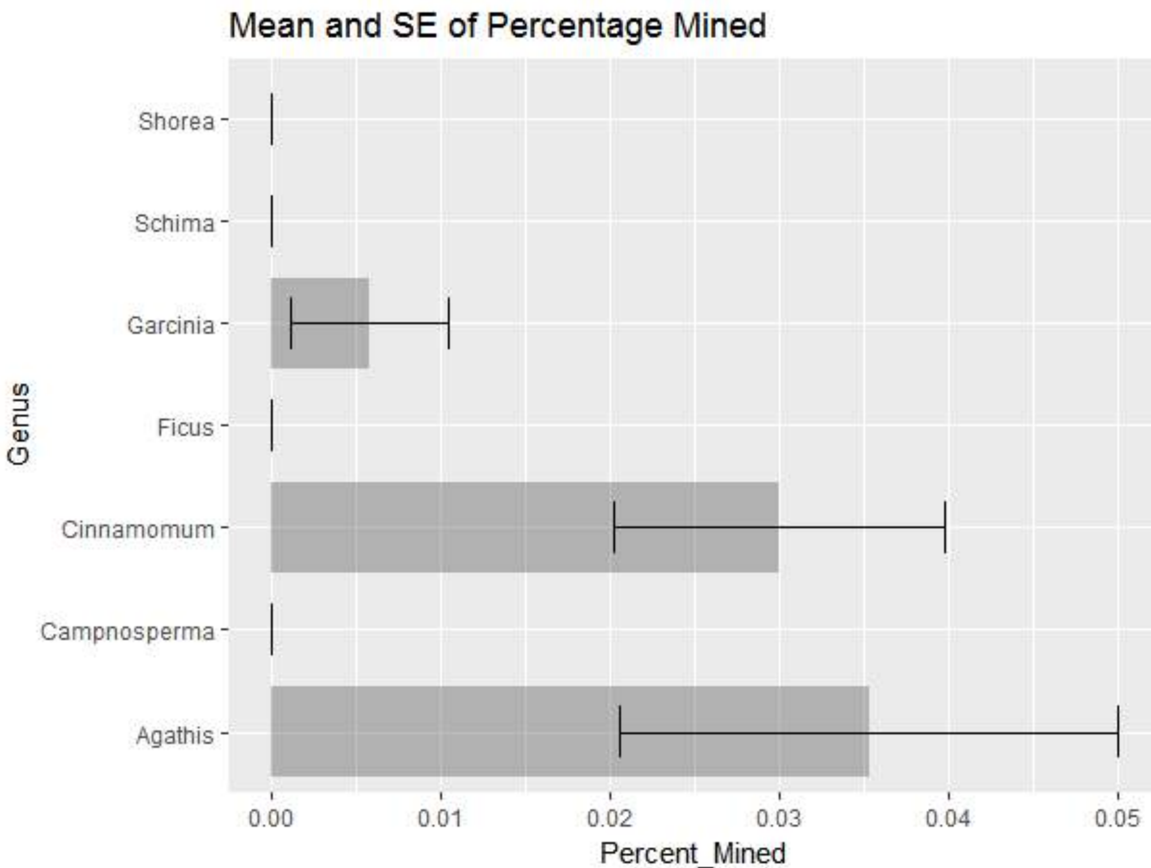

Figure 4. Mean percentage minded by genus (with Standard Errors).

An analysis of variance for the percentage eaten showed that genus was highly significant (F = 27.64, p-value < 2e-16; df= 6). The illustrated means and standard errors for each genus (Table 1 and Figure 3) show that two genera (*Cinnamomum* and *Campnosperma*) had much higher average herbivory than the other genera. An analysis of variance for the percentage mined similarly showed that genus was highly significant (F = 10.8, p-value = 9.8e-11; df= 6), meaning that there is considerable variability in leaf mining amongst the various genera (shown in Figure 4).

Herbivory and mining were also analyzed according to height (Figure 5), indicating that the mid-canopy appears to have the highest defoliation. More extensive sampling is required to confirm this initial observation.

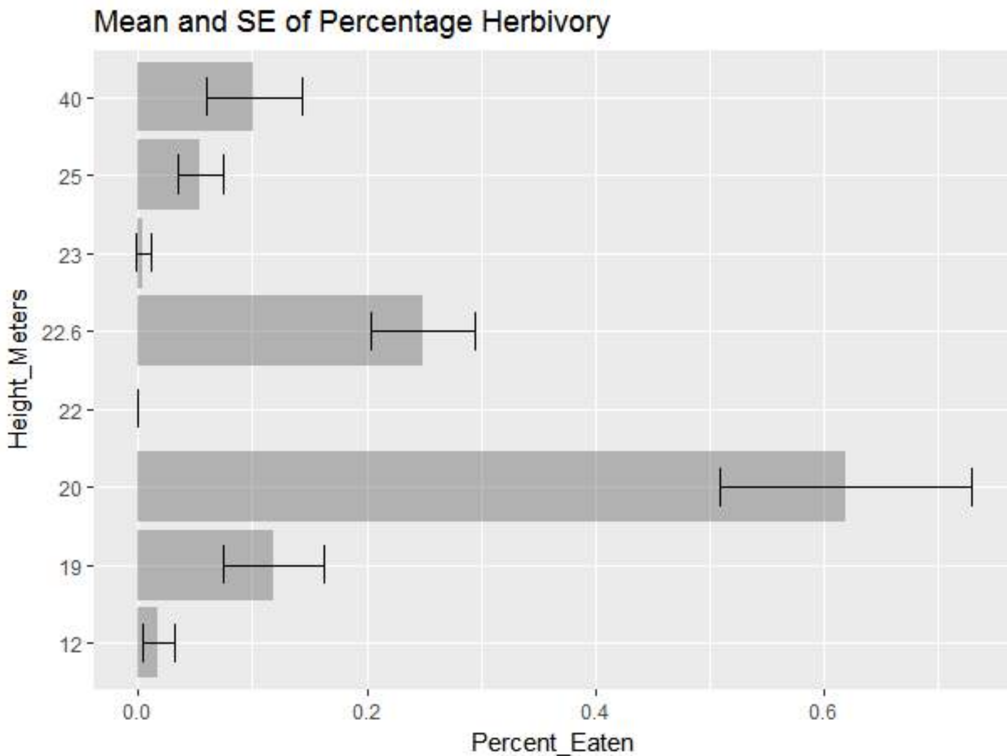

Figure 5. Percentage eaten according to height.

In addition, we compared summary statistics for Penang vs. Amazon data as shown in Table 2. An ANOVA for location (Penang vs. Amazon) and genus indicates that genera are highly significant ($F = 31.6$, p-value $< 2e-16$, $df=6$), but location is not ($F= 1.81$, p-value $= 0.18$, $df=1$). As shown in Table 2, the overall herbivory in Penang canopy trees averaged 11.2% (SE= 1.1) leaf area eaten, an indication that the insect herbivores comprise a healthy population. Leaf miners averaged 1.4% (SE =0.2) leaf surface area. No surveys of herbivorous arthropods, either chewing or leaf mining, were conducted during this time, however.

Table 2: Comparison of herbivory Penang vs. Amazon.

Location	Number of Records	Avg. Percent Eaten	Avg. Percent Mined	Eaten SE	Mined SE
Amazon	2,730	9.95	2.21	0.30	0.10
Penang	275	11.19	1.44	1.10	0.20

A more detailed genus and species comparison of Penang vs. Amazon data is shown in Table 3. Many more leaves were sampled in the Amazon, however, since the survey was conducted by a greater number of citizen science participants (2730 leaves in the Amazon versus 275 leaves in Penang). Herbivory was relatively similar in both canopies, averaging 9.9% in the Amazon and 11.2% in Penang. Leaf mining was reversed with 2.2% in Amazon and 1.4% in Penang.

Table 3: Detailed genus and species summary for Penang vs. Amazon.

Location	Genus	Species	Tree Number	Number of Records	Avg. Percent Eaten	Eaten SE	Avg. Percent Mined	Mined SE
Amazon	Aechmea	nallyi	13	145	10.3	0.8	6.2	0.6
Amazon	Apeiba	membranacea	9	105	10.7	1.9	1.6	0.2
Amazon	Cedrelinga	cateniformis	14	64	15.8	1.8	4	0.4
Amazon	Cedrelinga	cateniformis	18	58	12.4	2.9	3.5	0.4
Amazon	Diplotropis	martiusii	22	53	7.9	1.3	3.4	0.6
Amazon	Eschweilera	sp.	4	39	12	2.5	5	0.7
Amazon	Eschweilera	sp.	5	60	30.3	3.6	8.9	1.5
Amazon	Eschweilera	sp.	8	89	11.9	2.3	2.2	0.5
Amazon	Eschweilera	sp.	17	74	17.8	2.3	1.2	0.3
Amazon	Eschweilera	sp.	23	48	17	2.6	1.7	0.3
Amazon	Inga	sp.	12	62	10.9	0.8	9.9	2
Amazon	Inga	sp.	16	118	22.1	1.7	2	0.2
Amazon	Laconia	cymosa	1	106	4.7	0.6	1.4	0.2
Amazon	Osteophloeum	platyspermum	19	275	7	0.6	0.3	0
Amazon	Oxandra	xylopioides	3	365	0.9	0.2	0.3	0
Amazon	Oxandra	xylopioides	6	467	5	0.6	0.4	0.1
Amazon	Philodendron	sp.	24	22	20.4	2.5	6.7	1.2
Amazon	Pouteria	sp.	21	106	20.4	1.6	3.2	0.4
Amazon	Pterocarpus	rohrii	7	66	6.4	1.1	1.3	0.3
Amazon	Pterocarpus	rohrii	11	49	11.7	2.3	6	1.3
Amazon	Swartzia	polyphylla	20	61	34	2.8	6	0.5
Amazon	Terminalia	sp.	2	90	10.5	1.2	3	0.5
Amazon	Terminalia	sp.	10	125	9.1	1.4	1.2	0.2
Amazon	Virola	sp.	15	83	19.1	1.8	3.8	0.4
Penang	Agathis	borneesis	28	60	1.1	0.4	3.5	0.7
Penang	Campnosperma	auriculatum	31	25	24.9	2.2	0	0

Penang	Cinnamomum	porrectum	25	30	10.5	2.2	4.7	0.6
Penang	Cinnamomum	porrectum	32	20	61.9	5.3	0.4	0.2
Penang	Ficus	sp.	27	20	0	0	0	0
Penang	Garcinia	sp.	26	30	4.5	1.5	0	0
Penang	Garcinia	sp.	33	30	1.3	0.8	1.2	0.4
Penang	Schima	wallichii	29	30	11.8	2.2	0	0
Penang	Shorea	bracteolata	30	30	10.1	2.1	0	0

As a visual way of depicting herbivory, we used Tableau to create relative leaf sizes that visualize the levels of herbivory in descending order. We compared all Penang genera for both herbivory (Figure 6) and leaf mining (Figure 7) using a leaf icon.

Figure 6. Mean leaf area eaten by genus (Penang data).

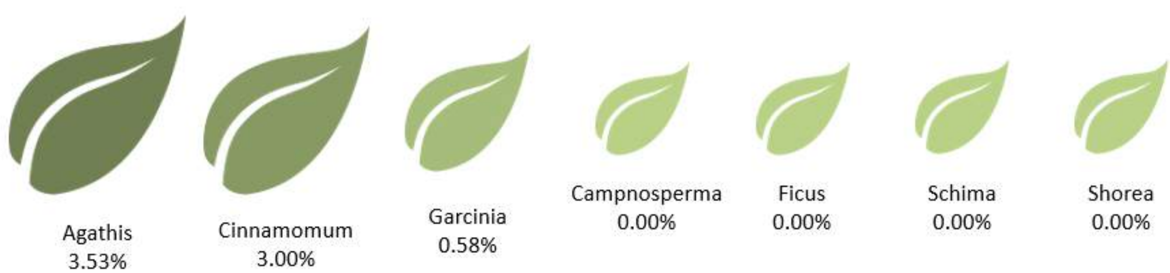

Figure 7. Mean leaf area mined by genus (Penang data).

In addition, we graphed herbivory and mining observations by species from Amazon and Penang datasets, as shown by Figure 8.

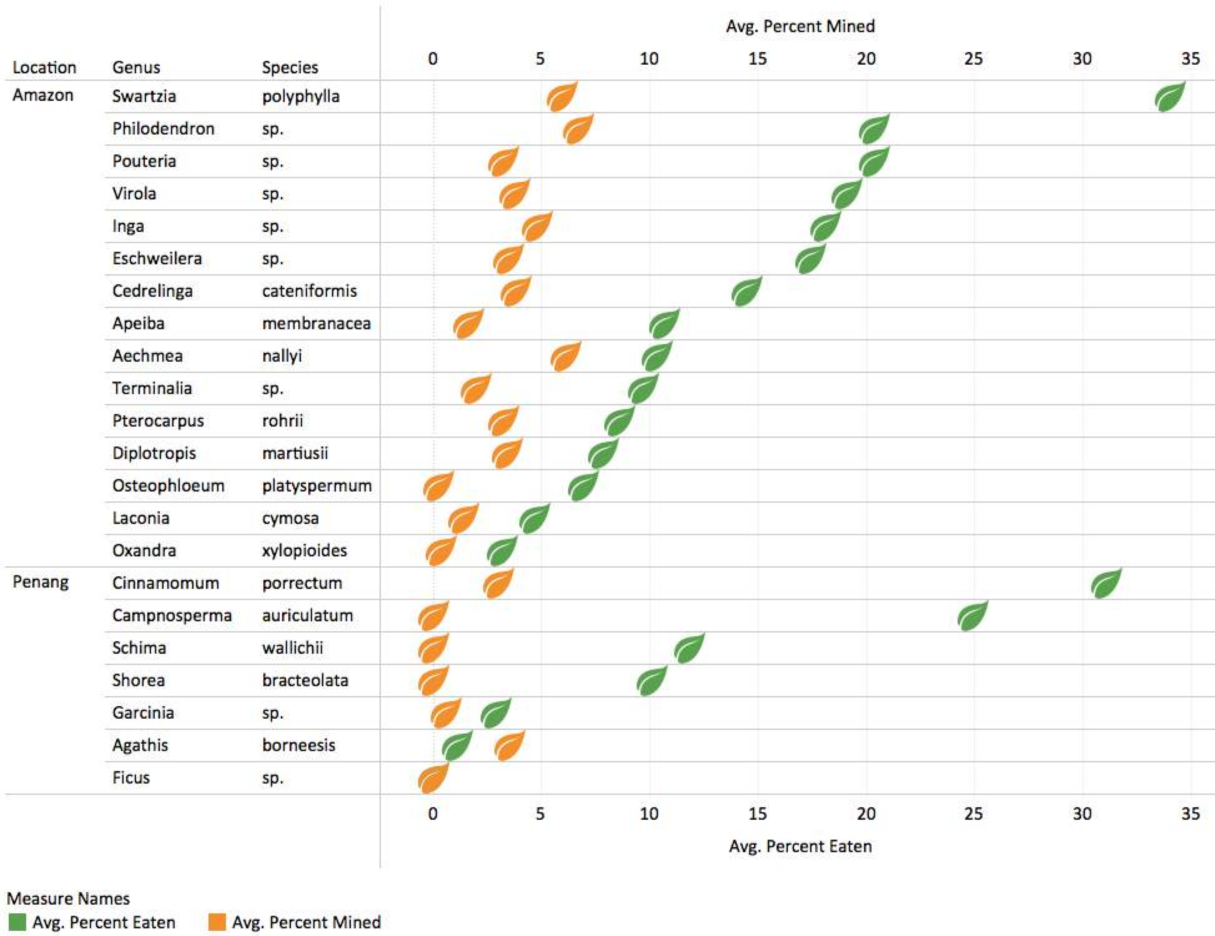

Figure 8. Mean leaf herbivory and mining by species.

Herbivory ranged from negligible to over 50% leaf area consumed in Penang but ranged from 3.2% to 34% in the Amazon. Mining was much less significant for both rain forest sites and for all species sampled except *Agathis borneesis*, which had slightly higher mining than defoliation.

All these leaf consumption figures are much higher than the early estimates of forest herbivory that were obtained from ground (only) sampling (e.g. Hairston et al 1960, Odum and Ruiz-Reyes 1970) and illustrate the importance of conducting whole forest surveys that include canopy foliage. Finally, these surveys represent snapshots, meaning the leaves were collected and measured at only one seasonal point in time. We therefore recognize that these amounts are underestimates of the real herbivory, because we did not sample over time and thereby measure foliage that was entirely or almost entirely eaten (Lowman 2014). In prior studies comparing long-term leaf data measurements with snapshot herbivory assessments, Lowman (2014) found that applying a multiplier of 2.1 to herbivory snapshot data can provide a relatively accurate amount of long-term herbivory, because the number of young leaves totally eaten is relatively consistent in tropical forest canopies. This suggests that the Penang Hill canopy may more accurately be 22.4 % leaf area eaten, if we were able to measure leaves a longer time frame.

Herbivory is a critical factor in forest canopy dynamics, because it essentially reduced the photosynthetic area of the ecosystem. This is an important economic drain on the tree, and the accuracy of herbivory measurements – from forest floor to uppermost canopy – are important to better understand the complexities of carbon storage, gas exchange, tree growth, and overall forest health. With the advancing degradation of Malaysian rain forests due to the oil palm industry, information about pristine Malaysian rain forest canopies is critical. Future management of these forests, especially reforestation, will require additional information about the plant-insect interactions at all levels within the forest, and for all types of vegetation. Canopy access remains a challenge in these tall tropical trees, but the technologies are improving for safe canopy access into *Dipterocarps*, *Shorea* and other important Asian species that remain relatively unstudied.

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References

Ernest KA, MD Lowman, HB Rinker and DC Shaw. 2006. Development of a novel method for assessing stand-level herbivory in forests. Newsletter of the International Canopy Network 12(2): 4-5.

Hairston NG, FE Smith, and LB Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94: 421-25.

Heatwole H, S Unsicker and MD Lowman. 2013. Ontogeny of herbivory on leaves in a tropical rain forest in Madagascar. IN: Treetops at Risk (eds. M Lowman, S Devy, and T Ganesh). Springer: 295-305.

Kaganovskiy L and MD Lowman. 2012. Mathematical modeling of forest canopies for herbivory. IN: Methods in Forest Canopy Research. MD Lowman, T Schowalter & J Franklin (eds.), University of California Press: 97-98.

Lowman MD 1984. An assessment of techniques for measuring herbivory: is rain forest defoliation more intense than we thought? Biotropica 16(4): 264-268.

Lowman MD. 1992. Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). Biotropica 24: 263-272.

Lowman MD. 1997. Herbivory in forests – from centimeters and megametres. Forests and Insects. AD Watt, NE Stork, and MD Hunter (eds.). Chapman & Hall: 135-49.

Lowman MD. 2012. Beetles in a salad bar: accurate assessment of herbivory in whole forests. IN: Methods in Forest Canopy research. MD Lowman, T Schowalter & J Franklin (eds.), University of California Press: 93-97.

Lowman MD. 2014. Calibrating discrete and long-term sampling methods for herbivory. In: Methods in Forest Canopy Research (eds. MD Lowman, T Schowalter, and J Franklin). Univ. California Press.

Lowman MD and JD Box 1983. Variation in leaf toughness and phonologic content among five species of Australian rain forest trees. Austr. J. Ecology 8: 17-25.

Lowman MD, RL Kitching, and G Carruthers. 1996. Arthropod sampling in Australian subtropical rain forest: how accurate are some of the more common techniques? Selbyana 17: 36-42.

Lowman MD and TD Schowalter. 2012. Plant science in forest canopies – the first 30 years of advances and challenges (1980-2010) New Phytologist 194(1): 12-27.

Lowman MD and HB Rinker. 2004a. Forest Canopies. Elsevier Publishers.

Lowman MD and HB Rinker. 2004b. Insect herbivory in tropical forests. IN: Forest Canopies. Elsevier Press, San Diego CA: 359-386.

Lowman MD, S Devy and T Ganesh. 2014. Treetops at Risk. Springer-Verlag.

Odum HT and J Ruiz-Reyes. 1970. Holes in leaves and the grazing control mechanism. IN: A Tropical Rain Forest (eds. HT Odum and RD Pigeon) pp. I-69-80. US Atomic Energy Commission, Oak Ridge TN.

Parker SS, GB Pauly, J Moore, NS Fraga, JJ Knapp, Z Principe, BV Brown, JM Randall, BS Cohen, and TA Wake. 2018. Adapting the BioBlitz to meet conservation needs. Conservation Biology 0: 1-13.

Shaw DC, KA Ernest, HB Rinker and MD Lowman. 2006. Stand-level herbivory in an old-growth conifer forest canopy. Western North American Naturalist 66(4): 473-81.

Voirin B, R Kays, M Wikelski, and MD Lowman. 2013. Why do sloths poop on the ground. IN: Treetops at Risk (eds. M Lowman, S Devy, and T Ganesh). Springer: 195-199