# Seasonal Changes in Vertical Stratification of Moth Diversity in Tropical Rainforests of Thailand

**Ronnarot Taveesri[a]\*, Akihiro Nakamura[b], Ekgachai Jeratthitikul[a], and Alyssa B. Stewart[c]**

[a]*Department of Biology, Faculty of Science, Mahidol University, Bangkok 10400, Thailand*
[b]*Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, China*
[c]*Department of Plant Science, Faculty of Science, Mahidol University, Bangkok 10400, Thailand*

## Abstract

Canopies of tropical rainforests present distinguished microclimates and habitats, creating vertically stratified forest biodiversity. Although distances from the ground to canopy layers are at most tens of meters, vertical turnover of communities are generally much greater than horizontal turnover which can stretch hundreds or thousands of meters. Insect diversity is stratified along vertical gradients, as insects, especially herbivorous insects, depend on various food resources and microhabitats provided by canopy trees. Although seasonal changes in insect community composition have been extensively documented, little attention has been paid to understand how vertical stratification of insects change across seasons. Here we investigated how moth diversity change vertically and horizontally across seasons in tropical rainforests located at different latitudes in Thailand. Moth samples were collected at Mo Singto (MS, 14º22′55″N 101º25′54″E) Khao Yai National Park, and Klong Naka Wildlife Sanctuary (KN, 9º27′34″N 98º30′15″E) in wet and dry seasons. At each site, moth samples were collected from the canopy and understory layers at a total of nine sampling plots established within a 300 m × 300 m grid. We identified moths to family as family level data can be compared across sites at different latitudes. The results showed that vertical stratification of moth diversity was more distinct in KN than MS plots, whereas seasonal change in moth diversity was more distinct in MS than KN. Our study suggests that vertical stratification of moth diversity is universal, as is suggested by other studies, but seasonal influence on vertical stratification may be highly variable across different latitudes.

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\*Corresponding Author: Ronnarot Taveesri
E-mail address: ronnarot.tav@student.mahidoal.ac.th

## 1. Introduction

Tropical rainforests are heterogeneous in microclimate and other habitat conditions across landscapes. Such heterogeneity is generally viewed horizontally, but there is an additional dimension in which microclimate and other habitat conditions are stratified vertically from forest floor to the canopy. Forest canopies are generally covered by tree crowns that act as sunlight filter and temperature insulator (Frenne et al., 2019; Lowman & Moffett, 1993). Insect species are distributed across space according to their own physical tolerance, resource-requirements and behavior (Wardhaugh, 2014). Thus, insect communities have been observed to change along not only horizontally but also vertically within tropical rainforests (Basset et al., 2015).

In the last few decades, β-diversity has gained much attention to be used as a tools to understand the mechanisms underlying the community assembly (Mori et al., 2018). Although β-diversity has recently been studied in a variety of ecosystems, canopy organisms did not gain attention due to limited accessibility to the canopy and the untested assumption that forest communities are more or less homogeneous across vertical gradients (Basset et al., 2003; Lowman et al., 1992). This assumption has been defied by recent studies that presented high heterogeneity of organisms along vertical strata (Ashton et al. 2016, Basset et al. 2012). These studies found that vertical, rather than horizontal dimension, explained changes in forest community composition. Moreover, tropical canopy was reported to harbour more and unique

species than understory (Lowman et al., 2013; Nakamura et al., 2017).

Previous studies of vertical diversity, however, overlooked how seasonal variation may influence vertical stratification of forest biodiversity (Ashton et al., 2016; Basham et al., 2019). Populations of tropical insect species are highly dynamic with varying abundance and activity periods across seasons (Wardhaugh, 2014). Although, tropical rainforests are recognized as a seasonal forests, temperature and rainfall change across seasons and the magnitude of such changes escalates with increasing latitude within tropical areas (Denlinger, 1986). Wet seasons provide higher precipitation (rainfall) resulting in increasing plant resources for insects (Poulin et al., 1999). Thus, peaks in insect abundance generally coincide with wet seasons when production of new leaves and flowers by many plant species occur (Basset, 1991; Frith & Frith, 1985).

Insects were commonly used as ecological models in β-diversity studies because they are key drivers of many ecological processes and predictors of environmental changes (Ashton et al., 2016; Nakamura et al., 2017). In this study, we focus on moths - common nocturnal insects that belong to the order Lepidoptera. They are one of the most widespread and species-rich insect groups in the world (Gaston, 1991). Moths are chosen because of the following reasons: moths are abundant and diverse insects which provide reliable statistical analysis; moths can be collected by automated light traps; and their herbivore feeding that links moths with plant spatial and temporal dynamics (Ashton et al., 2015; Basset et al., 2012).

This study aims to investigate how moth diversity is vertically stratified and how vertical stratification changes across latitudes and seasons in tropical rainforests of Thailand. This study presented the results of the influence of vertical stratification on moth β-diversity with seasonal changes through similarity, dispersion and distance-decay relationship of moth assemblage between strata. further, to investigate the consistency of changes in assemblage composition, 2 sampling plots were established in Mo Singto plot of Khao Yai National Park and Klong Naka wildlife sanctuary.

## 2. Methodology
### 2.1 Study site

Moths were collected inside the two protected tropical forest locations of Thailand. First sampling location was established in Mo Singto, Khao Yai National Park (MS, 14º22′55″N 101º25′54″E), Nakhon Ratchasima Province of northeastern Thailand. Second location was established in Klong Naka Wildlife sanctuary (KN, 9º27′34″N 98º30′15″E), Ranong Province of southern Thailand. In each location, a total of nine sampling plots were arranged as 3 × 3 grid points which were separated by 150 meters from each other (Figure 1). Sampling was conducted in two seasons at each location: sampling in Mo Singto was conducted in June (wet season) and December 2019 (dry season); and sampling in Klong Naka was conducted in March (dry season) and September 2020 (wet season).
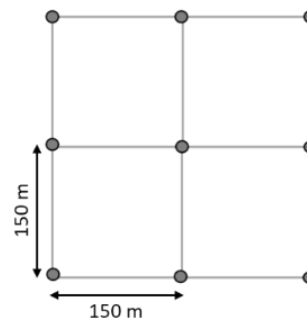


**Figure 1.** Diagram of the nine sampling plots established within each forest locations.

### 2.2 Sample collecting

Moths were collected using Pennsylvania-style light traps (Figure 2). At each sampling plot, moths were collected from the forest canopy and understory. One light trap was set immediately below the canopy surface at least 20 m above the ground but the height varied depending on the tree height (generally higher in KN than MS). Another trap was set two meters above the ground. Light traps were hoisted using a white rope which was suspended by the tree branches. For the canopy traps, we used a Big Shot Line Launcher (WesSpur Bellingham WA) to suspend the ropes over the tree branches.

Traps were running for a total of three nights during the sampling season but avoided seven days before and after full moon. Traps were retrieved next day of the light trapping and specimens were kept in the plastic containers (with tissue papers) and left in a deep freezer (-20°C). Temperature and light intensity (lux) were measured using HOBO pendant data loggers suspended in the canopy and understory at each plot for 3-6 months after moth sampling was completed. Canopy height was recorded using a handheld laser clinometer (HT-900A Compact).



**Figure 2.** Pennsylvania light traps with Philips TL 8W actinic BL light bulb

## 2.3 Sample processing

Macro-moths (>2 cm wing spans) were selected as target insects. All macro-moths were identified to family using morphological key of *The Moths of Borneo* (Holloway, 1983). Other non-target insects were preserved in 95% ethanol.

## 2.4 Statistical analysis

Macro-moth families and their abundances from each stratum (canopy or understory) at each sampling plot across two locations and seasons were used as sample unit used for statistical analysis. Three sampling nights from each sampling season were pooled. We therefore obtained a total of: 2 locations×2 seasons×9 sampling plots×2 strata=72 samples We first estimated sampling sufficiency and gamma diversity of moth families collected from different vertical strata and seasons in MS and

KN locations by generating rarefaction curves using *iNEXT* package (Hsieh et al., 2016) in R program (Project R for Statistical Computing). We generated individual-based rarefaction curves by plotting family richness against a number of individuals. Extrapolation was also made by doubling the number of observed individuals to estimate moth family richness.

Beta diversities were calculated using Horn dissimilarity index. Horn dissimilarity index quantifies the overlap of species among sampling units which could reduce bias caused by rare or dominated species (Jost, 2007). To test the influence of three main factors (Vertical stratum, Seasonal changes and Forest type) and their interactions on moth assemblages, we ran PERMANOVA tests using *adonis2* function of *vegan* package with 9999 permutations of samples (Anderson, 2001; Oksanen et al., 2019). Then assemblages between canopies and understories were compared across different seasons and forests via post-hoc pairwise analysis using *pairwise.adonis* functions of *pairwiseAdonis* package (Oksanen et al., 2019). Additionally, as vertical stratification could differently affect moths in each family, we performed similarity percentages analysis using *SIMPER* of *vegan* package (Oksanen et al., 2019) to detect moth families that significantly changed their abundance and occurrence frequencies among groups of samples. NMDs plots were generated to visualize changes in moth assemblage composition between vertical strata and seasons. They were created by *metaMND* function of *vegan* package (Faith et al., 1987).

Horizontal beta diversity (measured as average distances of moth assemblage samples from the centroids of the group distances) in moth diversity was quantified within canopy and understory strata across two locations *beta.disper* function on *vegan* package and tested by ANOVA (Anderson, 2006). Distance-decay relationships (pair-wise horizontal distances plotted against pair-wise distance measures between samples) were investigated using *decay.model* function of *betapart* package (Nekola & Mcgill, 2014).

Variation portioning were analyzed to investigate how much variation in the moth

assemblage composition was explained by seasons, horizontal distance and vertical distance in MS and KN (two locations analyzed separately) using *varpart* function on vegan package (Borcard et al., 1992).

## 3. Results

### *3.1 Abundance and family richness*

We collected a total of 13723 moths belonging to 13 families in this study. Mean abundance of wet season moth was higher than dry season in both Mo Singto (MS) and Klong Naka plot (KN). MS plot showed higher mean abundance of moth in canopy than understory in wet season with no difference in dry season. In contrast, KN plots showed higher mean abundance of moth in understory than canopy in wet season with no difference in dry season (Figure 3).

Individual-based rarefaction curves showed that MS plot had higher number of families in canopy than understory in wet season, but their 95% confidence intervals overlapped, suggesting that the differences were not significant. Similar trajectories were found in canopy and understory of dry season which showed lower than the wet season. Extrapolating to twice the number of individuals didn't present different trends (Figure 4a). In Klong Naka plot, although smaller number of individuals were collected in dry than wet seasons, both canopy and understory samples from wet and dry seasons showed similar trajectories with similar number of families, and extrapolating to twice the number of individuals did not change the observed trends (Figure 4b).
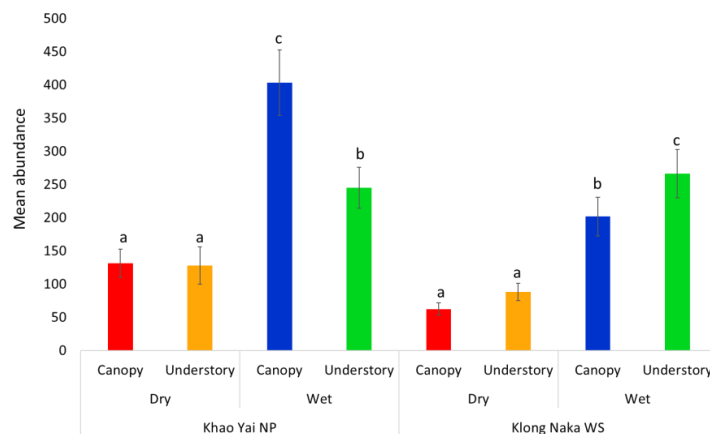


**Figure 3.** Mean abundance of moths in each vertical stratum and seasons in Mo Singto (MS) Khao Yai NP (left) and Klong Naka (KN) Wildlife Sancturat (right).
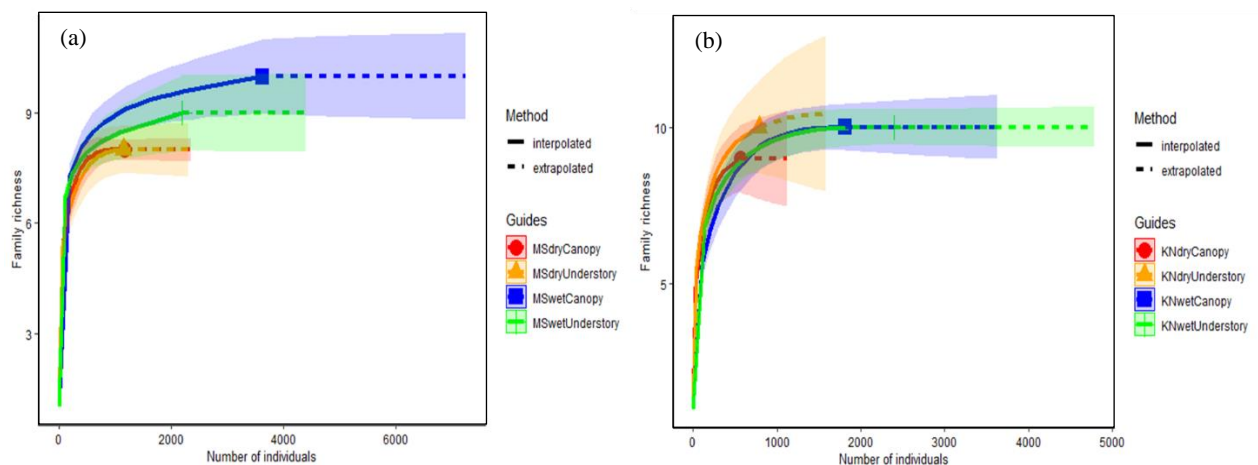


**Figure 4.** Individual-based rarefaction curves of moth family richness in canopy and understory samples collected in dry and wet seasons in: a=Mo Singto plots; and b=Klong Naka plots.

## 3.2 PERMANOVA

PERMANOVA analysis indicated that moth communities were significantly explained by vertical stratum, locations and seasons. Three-way interaction of those factors was observed (Table 1). Post-hoc PERMANOVA showed that vertical stratification of moth was influenced by sampling area and seasons with different pattern (Table 2).

**Table 1.** PERMANOVA results based on Horn dissimilarities using family data for moth community structure in relation to compartment for vertical stratum (canopy and understory), locations (Mo Singto and Klong Naka plot) and seasonality (wet and dry season).

| Factor | Df | Sum of Sqs | R2 | F | Pr(>F) | |
|---|---|---|---|---|---|---|
| Vertical | 1 | 0.099 | 0.142 | 18.360 | 0.001 | *** |
| Location | 1 | 0.089 | 0.127 | 16.467 | 0.002 | ** |
| Season | 1 | 0.123 | 0.176 | 22.834 | 0.001 | *** |
| Vertical: Location | 1 | -0.030 | -0.043 | -5.584 | 1 | |
| Vertical: Season | 1 | 0.028 | 0.040 | 5.194 | 0.065 | . |
| Vertical: Location: Season | 1 | 0.039 | 0.055 | 7.150 | 0.018 | * |
| Residual | 65 | 0.352 | 0.502 | | | |
| Total | 71 | 0.701 | 1 | | | |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

**Table 2.** Post-hoc PERMANOVA results compared moth communities between canopy and understory.

| Locations and seasons | Df | Sums Of Sqs | F.Model | R2 | p.value | p.adjusted | |
|---|---|---|---|---|---|---|---|
| MS Wet | 1 | 0.038 | 8.934 | 0.358 | 0.028 | 0.028 | . |
| MS Dry | 1 | 0.002 | 0.321 | 0.020 | 0.544 | 0.544 | |
| KN Wet | 1 | 0.007 | 20.231 | 0.558 | 0.001 | 0.001 | ** |
| KN Dry | 1 | 0.097 | 30.523 | 0.656 | 0.001 | 0.001 | ** |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

## 3.3 Similarity percentages of moth communities along vertical stratum

In MS wet season, similarity percentages showed that 5 of 10 moth families, namely Crambidae (P<0.001), Noctuidea (P<0.05), Cossidae (P<0.05), Erebidae (P<0.1) and Saturnidea (P<0.1) (Table 3), were vertically significantly different and higher in the canopy. In MS dry season, only Bombycidae was significantly higher in the canopy (P<0.1) (Table 4).

In KN wet season, similarity percentages showed that 4 of 11 moth families, namely Zygaenidea (P>0.001), Geometridae (P>0.01), Notodontidae (P>0.01) and Lasiocampidae (P>0.05) (Table 5), were vertically significantly different and greater in the understory. In KN dry season, 3 of 9 moth families, namely Erebidae (P>0.01), Geometridae (P>0.01) and Notodontidae (P>0.01) (Table 6), were greater in the understory.

**Table 3.** Similarity percentages of moth family communities between canopy and understory of Mo Singto wet season

| Family | average | sd | ratio | canopy | understory | P-value | |
|---|---|---|---|---|---|---|---|
| Crambidae | 0.160 | 0.074 | 2.158 | 172.556 | 75.889 | 0.001 | *** |
| Geometridae | 0.079 | 0.061 | 1.291 | 89.556 | 82.222 | 0.999 | |
| Noctuidea | 0.055 | 0.039 | 1.413 | 59.556 | 27.667 | 0.03 | * |
| Erebidae | 0.044 | 0.028 | 1.567 | 64.444 | 44 | 0.055 | . |
| Notodontidae | 0.010 | 0.007 | 1.319 | 7.333 | 9 | 0.112 | |
| Sphingidae | 0.006 | 0.006 | 0.966 | 5.444 | 3.667 | 0.57 | |
| Lasiocampidae | 0.003 | 0.003 | 1.078 | 2.556 | 1.667 | 0.646 | |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

**Table 3.** Similarity percentages of moth family communities between canopy and understory of Mo Singto wet season (cont.)

| Family | average | sd | ratio | canopy | understory | P-value | |
|---|---|---|---|---|---|---|---|
| Bombycidea | 0.002 | 0.002 | 1.007 | 1 | 0.556 | 0.843 | |
| Saturniidae | 0.001 | 0.0008 | 0.878 | 0.444 | 0.111 | 0.079 | . |
| Cossidae | 0.0001 | 0.0004 | 0.348 | 0.111 | 0 | 0.015 | * |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

**Table 4.** Similarity percentages of moth family communities between canopy and understory of Mo Singto plot dry season

| Family | average | sd | ratio | canopy | understory | P-value | |
|---|---|---|---|---|---|---|---|
| Crambidae | 0.130 | 0.094 | 1.389 | 54.333 | 49.556 | 0.84 | |
| Erebidae | 0.114 | 0.080 | 1.419 | 39.556 | 42.667 | 0.945 | |
| Geometridae | 0.060 | 0.055 | 1.075 | 16.778 | 16.778 | 0.931 | |
| Noctuidea | 0.041 | 0.029 | 1.442 | 16.778 | 14.556 | 0.799 | |
| Notodontidae | 0.012 | 0.010 | 1.188 | 2.333 | 3.222 | 0.39 | |
| Sphingidae | 0.003 | 0.005 | 0.603 | 0.556 | 0.556 | 0.558 | |
| Lasiocampidae | 0.002 | 0.003 | 0.797 | 0.444 | 0.444 | 0.641 | |
| Bombycidea | 0.002 | 0.004 | 0.551 | 0.444 | 0 | 0.091 | . |
| Zygaenidea | 0.001 | 0.002 | 0.467 | 0 | 0.222 | 0.345 | |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

**Table 5.** Similarity percentages of moth family communities between canopy and understory of Klong Naka plot wet season

| Family | average | sd | ratio | canopy | understory | P-value | |
|---|---|---|---|---|---|---|---|
| Crambidae | 0.125 | 0.088 | 1.418 | 110.889 | 144.778 | 0.221 | |
| Geometridae | 0.061 | 0.038 | 1.621 | 19 | 45.333 | 0.005 | ** |
| Erebidae | 0.052 | 0.036 | 1.447 | 56.444 | 51.778 | 1 | |
| Noctuidea | 0.016 | 0.014 | 1.148 | 11.222 | 13.444 | 0.647 | |
| Notodontidae | 0.008 | 0.007 | 1.225 | 1.667 | 5.333 | 0.006 | ** |
| Zygaenidea | 0.005 | 0.004 | 1.318 | 0 | 2.667 | 0.001 | *** |
| Lasiocampidae | 0.003 | 0.002 | 1.345 | 0.556 | 1.444 | 0.043 | * |
| Delceridae | 0.002 | 0.002 | 0.798 | 0.444 | 0.556 | 0.116 | |
| Bombycidea | 0.001 | 0.001 | 1.004 | 0.556 | 0.444 | 0.987 | |
| Saturniidae | 0.001 | 0.001 | 0.909 | 0.444 | 0.333 | 0.974 | |
| Sphingidae | 0.0005 | 0.001 | 0.495 | 0.222 | 0 | 0.473 | |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

**Table 6.** Similarity percentages of moth family communities between canopy and understory of Klong Naka plot dry season

| Family | average | sd | ratio | canopy | understory | P-value | |
|---|---|---|---|---|---|---|---|
| Crambidae | 0.110 | 0.078 | 1.407 | 32.444 | 30.444 | 0.994 | |
| Erebidae | 0.107 | 0.069 | 1.551 | 13.778 | 28.444 | 0.003 | ** |
| Geometridae | 0.084 | 0.057 | 1.487 | 5.222 | 18 | 0.008 | ** |
| Noctuidea | 0.034 | 0.027 | 1.254 | 8.667 | 7 | 0.635 | |
| Notodontidae | 0.012 | 0.008 | 1.472 | 0.333 | 2.111 | 0.009 | ** |
| Delceridae | 0.007 | 0.006 | 1.024 | 0.778 | 0.667 | 0.263 | |
| Bombycidea | 0.005 | 0.006 | 0.850 | 0.444 | 0.556 | 0.923 | |
| Lasiocampidae | 0.004 | 0.004 | 0.954 | 0.444 | 0.444 | 0.922 | |
| Sphingidae | 0.001 | 0.003 | 0.615 | 0.111 | 0.222 | 0.501 | |
| Limacodidae | 0.0006 | 0.002 | 0.348 | 0ʰ | 0.111 | 0.106 | |

Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1

### 3.4 NMDs ordination

NMDs ordination showed that, in MS, moth assemblages between the canopy and understory in wet season trended to be more dissimilar than those between canopy and understory in dry season. Moth communities between wet and dry seasons were obviously separated. At KN, moth assemblages between understory and canopy separated, but dry season moth assemblages were similar to the canopy samples collected in wet season. In contrast, wet season understory moths assemblages were distinctively different from others (Figure 5).

### 3.5 Beta dispersion

Beta dispersion found no significant differences in dispersion between the canopy and understory strata (Table 7) across locations and seasons. Significant distance-decay relationship was found only in wet season of canopy moths in Mo Singto ($P>0.01$) (Figure 6).
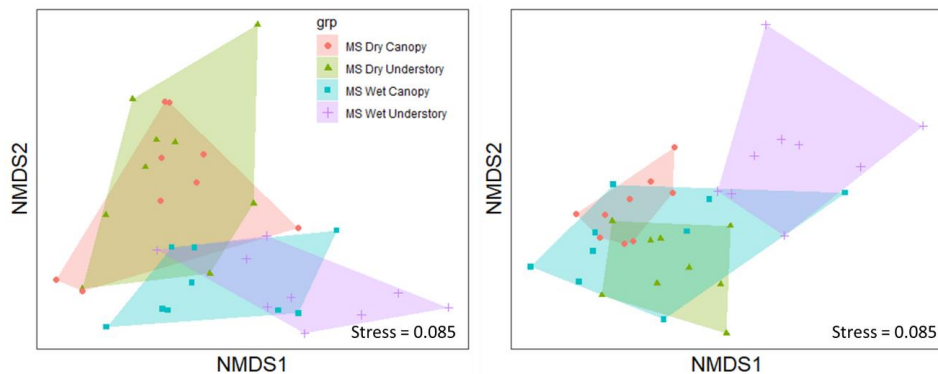


**Figure 5.** NMDs ordination of moth assemblages (based on Horn distance index) collected from the canopy and understory in wet and dry seasons. MS (left) and KN (right) locations were presented separately. Which points represented each community within their vertical layers and seasons.

**Table 7.** Beta dispersion of horizontal moth assemblage between canopy and understory.

| Habitat | | Df | Sum Sq | Mean Sq | F value | Pr(>F) |
|---------|--|----|--------|---------|---------|--------|
| MS Wet | Groups | 1 | 0.000319 | 0.000319 | 0.1709 | 0.6848 |
| | Residuals | 16 | 0.029821 | 0.001864 | | |
| MS Dry | Groups | 1 | 0.000063 | 6.35E-05 | 0.0217 | 0.8848 |
| | Residuals | 16 | 0.046847 | 2.93E-03 | | |
| KN Wet | Groups | 1 | 5.48E-05 | 5.48E-05 | 0.3061 | 0.5877 |
| | Residuals | 16 | 0.002864 | 1.79E-04 | | |
| KN Dry | Groups | 1 | 0.000234 | 2.34E-04 | 0.1567 | 0.6974 |
| | Residuals | 16 | 0.023898 | 1.49E-03 | | |

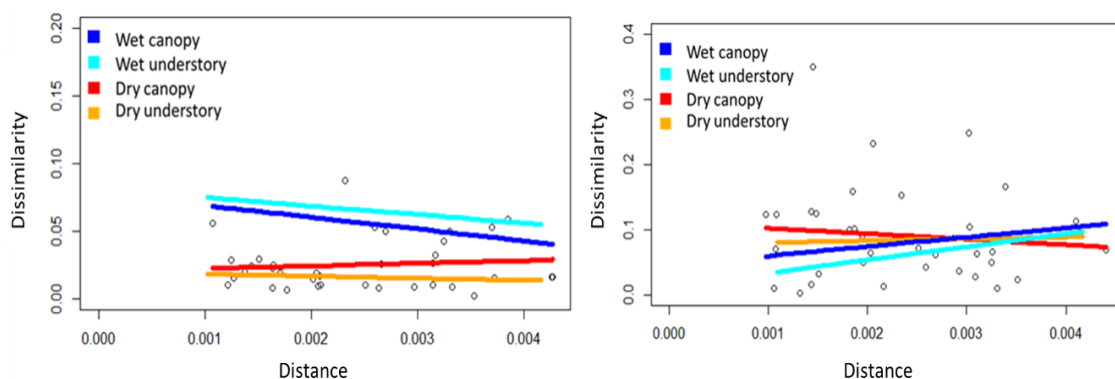Significant codes: '***' = P>0.001; '**' = P>0.01; '*' = P>0.05; '.' = P>0.1; ' ' = P>1



**Figure 6.** Distance-decay of moth communities along horizontal distance in each vertical Table stratum, sampling area and seasons.

### 3.6 Variation partitioning

In MS, moth assemblages were mostly explained by seasons (75.2%) and vertical distance (10.9%). In KN, assemblage variation was explained by vertical distance (23.2%) and seasons (16.5%). Very small proportions of moth assemblage composition were explained by horizontal distance in both Mo Singto (4.7%) and Klong Naka (4.2%). Note that more variation was explained in MS (45.4% residuals) than KN location (64.1% residuals) (Figure 7).
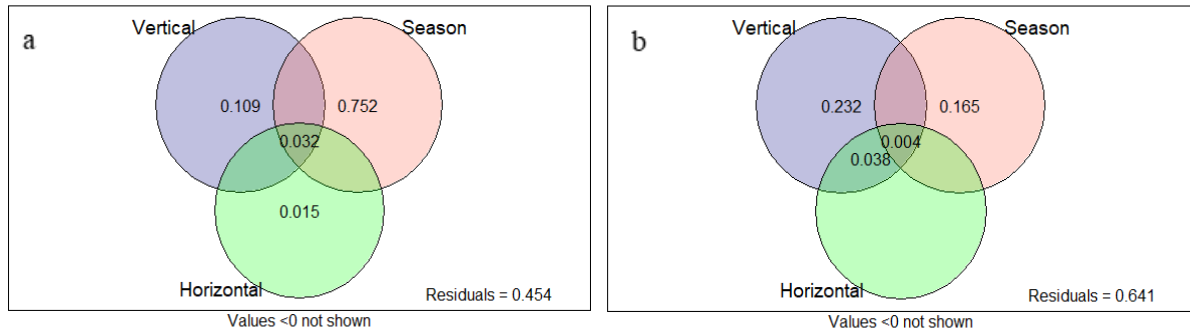


**Figure 7.** Venn diagram displaying proportions of variations in moth assemblage composition explained by seasons and vertical and horizontal distances in MS (a) and KN (b) locations. As Horn distance index was not Euclidean distances, some correlation coefficients returned negative values (not shown) and, as a result, explained variations and residuals do not add up to 1. (a=Mo Singto plot, b=Klong Naka plot)

## 4. Discussion

The results revealed the evidence that moth communities changed along vertical dimension and across seasons (Table 1). Vertical stratification was found in the results of moth community dissimilarity and characteristic moth families primarily found in the canopy or understory. Patterns in vertical stratification and seasonal influence were, however, different between the two locations (Table 2-6, Figure 5). Moth communities were explained by vertical distances and seasonal changes, whereas little variation was explained by horizontal distances (Figure 7). Moreover, moth assemblage dispersion and distance-decay relationships (both in horizontal dimension) were non-significant (Table 7 and Figure 6).

The results showed clear vertical stratification in moth communities. Canopy moth communities differed from understory moth communities, and the same patterns were found elsewhere (Nice et al., 2019). Forest canopies created different habitat structures, physical conditions and plant communities which vary through vertical gradients. Moths were influenced by forest structures and openness. Canopy gaps create space to access the food and provide mating resource which was important to rainforest lepidopterans (Delabye et al., 2021; Vlasanek et al., 2013). Plant diversity could play an important role for enhancing moth diversity. Indeed, previous studies showed that vertical stratification of plant species created vertical stratification of lepidopterans (Aduse-Poku et al., 2012).

Seasonal changes affected moth abundance and community composition. At Mo Singto, moth assemblages between seasons had low similarity. Wet season increased the magnitude of vertical stratification. Seasonal changes are associated with weather conditions such as rainfall, temperature, wind, radiation and plant phenology. Those factors may have had effects on the distribution of arthropods (Grimbacher & Stork, 2009; Poulin et al., 1999). However, this study only collected samples in only one months for each season and was not monthly surveys which could represent the gradual changes in moth community through time.

Mo Singto and Klong Naka locations were different in forest type, weather and unique species. Mo Singto is located in northern-east part of Thailand with seasonal evergreen forests. Due to northern-east weather condition, wet season is in summer (June to October) and dry

season in winter (November - February). Whereas, Klong Naka is located in southern Thailand which generaly has rainy season from May to October and dry season from November to April. Klong Naka forest had smaller seasonal changes in plant phenology and forest structures than Mo Singto. Therefore, seasonal influences are more pronounced in the Mo Singto than Klong Naka, as was seen in the results of variation partitioning (variation in moth assemblages explained by seasonal differences: MS, 75.9%; KN, 16.5%) (Figure 7). Moreover, Klong Naka plots showed greater magnitude of vertical stratification than Mo Singto (Table 2, Figure 5). Vertical stratification of diversity may increase with decreasing latitude, and this could be driven by increasing forest structural complexity, vegetation diversity and canopy height in the equatorial tropical rainforests (Lieberman et al., 1996).

Unfortunately, horizontal distance did not explain moth communities. Due to our taxonomic resolution at moth family and not species, it is possible that our limited taxonomic resolution could not be used to differentiate horizontal moth communities. On the other hand, our limited taxonomic resolution was still sufficient to detect vertical stratification and seasonal changes across the two locations at different latitudes.

## 5. Conclusions

Moth community was highly influenced by vertical stratum and seasonal changes, but the magnitude of differences depend on the forest type and latitude. Vertical stratification of moths was confirmed by community dissimilarity and some moth families unequally distributed along vertical strata. Seasonal differences were related to increasing vertical stratification of moth. This study represented the importance of seasonal variation and forest types on vertical stratification study in tropical rainforests.

## Acknowledgement

## References

Aduse-Poku, K., William, O., Oppong, S. K., Larsen, T., Ofori-Boateng, C., & Molleman, F. (2012). Spatial and temporal variation in butterfly biodiversity in a West African forest: Lessons for establishing efficient rapid monitoring programmes. *African Journal of Ecology*, *50*(3), 326-334.

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32-46.

Anderson, M. J. (2006). Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*, *62*(1), 245-253.

Ashton, L. A., Barlow, H. S., Nakamura, A., & Kitching, R. L. (2015). Diversity in tropical ecosystems: The species richness and turnover of moths in Malaysian rainforests. *Insect Conservation and Diversity*, *8*(2), 132-142.

Ashton, L. A., Nakamura, A., Basset, Y., Burwell, C. J., Cao, M., Eastwood, R., Odell, E., de Oliveira, E. G., Hurley, K., Katabuchi, M., Maunsell, S., Mcbroom, J., Schmidl, J., Sun, Z., Tang, Y., Whitaker, T., Laidlaw, M. J., Mcdonald, W. J. F., & Kitching, R. L. (2016). Vertical stratification of moths across elevation and latitude. *Journal of Biogeography*, *43*(1), 59-69.

Basham, E. W., Seidl, C. M., Andriamahohatra, L. R., Oliveira, B. F., & Scheffers, B. R. (2019). Distance–decay differs among vertical strata in a tropical rainforest. *Journal of Animal Ecology*, *88*(1), 114-124.

Basset, V., Cizek, L., Cuénoud, P., Didham, R. K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J., Tishechkin, A. K., Winchester, N. N., Roubik, D. W., Aberlenc, H. P., Bail, J., Barrios, H., Bridle, J. R., Castaño-Meneses, G., Corbara, B., … Leponce, M. (2012). Arthropod diversity in a tropical forest. *Science*, *338*(6113), 1481-1484.

Basset, Y. (1991). The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecological Entomology*, *16*(3), 265-278.

Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Novotny, V., Ødegaard, F., Roslin, T., Tishechkin, A. K., Schmidl, J., Winchester, N. N., Roubik, D. W., Aberlenc, H. P., Bail, J., Barrios, H., Bridle, J. R., Castaño-Meneses, G., Corbara, B., Curletti, G., Duarte Da Rocha, W., … Leponce, M. (2015). Arthropod distribution in a tropical rainforest: Tackling a four dimensional puzzle. *PLoS ONE*, *10*(12), 1-22.

Basset, Y., Hammond, P. M., Barrios, H., Holloway, J. D., & Miller, S. E. (2003). Vertical stratification of arthropod assemblages. In *Arthropods of tropical*

*forests: spatio-temporal dynamics and resource use in the canopy.*

Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the Spatial Component of Ecological Variation Author (s): Daniel Borcard , Pierre Legendre and Pierre Drapeau Published by : Ecological Society of America PARTIALLING OUT THE SPATIAL COMPONENT OF ECOLOGICAL VARIATION1. *Ecology*, *73*(3), 1045-1055.

de Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under forest canopies. *Nature Ecology and Evolution*, *3*(5), 744-749.

Delabye, S., Maicher, V., Sáfián, S., Doležal, J., Altman, J., Janeček, Š., Kobe, I. N., Murkwe, M., Šebek, P., & Tropek, R. (2021). Butterfly and moth communities differ in their response to habitat structure in rainforests of Mount Cameroon. *Biotropica*, *53*(2), 567-580.

Denlinger, D. L. (1986). Dormancy in tropical insects. *Annual Review of Entomology. Vol. 31*, 239-264.

Faith, D. P., Minchin, P. R., & Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, *69*(1–3), 57-68.

Frith, C. B., & Frith, D. W. (1985). Seasonality of insect abundance in an Australian upland tropical rainforest. *Australian Journal of Ecology*, *10*(3), 237–248.

Gaston, K. J. (1991). The Magnitude of Global Insect Species Richness. *Conservation Biology*, *5*(3), 283-296.

Grimbacher, P. S., & Stork, N. E. (2009). Seasonality of a diverse beetle assemblage inhabiting lowland tropical rain forest in australia. *Biotropica*, *41*(3), 328-337.

Holloway, J. D. (1983). *The Moths of Borneo: Key to families; families Cossidae, Metarbelidae, Ratardidae, Dudgeoneidae, Epipyropidae and Limacodidae*. Malaysian Nature Society.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*.

Jost, L. (2007). Partitioning Diversity into Independent Alpha and Beta Components. *Ecology*, *88*(10), 2427–2439.

Lieberman, D., Lieberman, M., Peralta, R., & Hartshorn, G. S. (1996). Tropical Forest Structure and Composition on a Large-Scale Altitudinal Gradient in Costa Rica. *The Journal of Ecology*, *84*(2), 137.

Lowman, M., Devy, S., & Ganesh, T. (2013). Treetops at risk: Challenges of global canopy ecology and conservation. In *Treetops at Risk: Challenges of Global Canopy Ecology and Conservation*.

Lowman, M., & Moffett, M. (1993). The ecology of tropical rain forest canopies. *Trends in Ecology and Evolution*, *8*(3), 104-107.

Lowman, M., Taylor, P., & Block, N. (1992). Vertical stratification ofsmall mammals and insects in the canopy of a temperate deciduous forest: A reversal of tropical forest distribution? *Selbyana*, *14*, 25.

Mori, A. S., Isbell, F., & Seidl, R. (2018). β-Diversity, Community Assembly, and Ecosystem Functioning. *Trends in Ecology and Evolution*, *33*(7), 549-564.

Nakamura, A., Kitching, R. L., Cao, M., Creedy, T. J., Fayle, T. M., Freiberg, M., Hewitt, C. N., Itioka, T., Koh, L. P., Ma, K., Malhi, Y., Mitchell, A., Novotny, V., Ozanne, C. M. P., Song, L., Wang, H., & Ashton, L. A. (2017). Forests and Their Canopies: Achievements and Horizons in Canopy Science. *Trends in Ecology and Evolution*, *32*(6), 438-451.

Nekola, J. C., & Mcgill, B. J. (2014). Scale dependency in the functional form of the distance decay relationship. *Ecography*, *37*(4), 309-320.

Nice, C. C., Fordyce, J. A., Bell, K. L., Forister, M. L., Gompert, Z., & DeVries, P. J. (2019). Vertical differentiation in tropical forest butterflies: A novel mechanism generating insect diversity? *Biology Letters*, *15*(1).

Oksanen, A. J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., Hara, R. B. O., Simpson, G. L., Solymos, P., Stevens, M. H. H., & Szoecs, E. (2019). Vegan. *Encyclopedia of Food and Agricultural Ethics*, 2395-2396.

Poulin, B., Wright, S. J., Lefebvre, G., & Calderón, O. (1999). Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *Journal of Tropical Ecology*, *15*(2), 213-227.

Vlasanek, P., Sam, L., & Novotny, V. (2013). Dispersal of butterflies in a New Guinea rainforest: Using mark-recapture methods in a large, homogeneous habitat. *Ecological Entomology*, *38*(6), 560-569.

Wardhaugh, C. W. (2014). The spatial and temporal distributions of arthropods in forest canopies: Uniting disparate patterns with hypotheses for specialisation. *Biological Reviews*, *89*(4), 1021-1041.