

Ant assemblage turnover is greater horizontally than vertically in the world's tallest tropical forest

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Abstract

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Abstract

Abiotic and biotic factors structure species assembly in ecosystems both horizontally and vertically. However, the way community composition changes along comparable horizontal and vertical distances in complex three-dimensional habitats, and the factors driving these patterns, remain poorly understood. By sampling ant assemblages at comparable vertical and horizontal spatial scales in a tropical rain forest, we compared observed patterns with those predicted according to environmental filtering by microclimate and microhabitat structure. We found that although dissimilarity between ant assemblages increased with vertical distance, the dissimilarity was higher horizontally but was independent of distance. The pronounced horizontal and vertical structuring of ant assemblages across short distances is likely explained by a combination of microclimate and microhabitat connectivity. Our results demonstrate the importance of considering three-dimensional spatial variation in local assemblages and reveal how highly diverse communities can be supported by complex habitats.

Keywords : community ecology, distance-decay, habitat complexity, microclimate, species turnover, vertical stratification

Introduction This turnover of ecological communities occurs in both vertical and horizontal dimensions (Sreekar et al. 2017), which can be explained by both biotic and abiotic factors, as well as their interactions (Cottenie 2005). The relative importance of these processes in determining community composition varies with spatial scale (Nekola and McGill 2014). At small spatial scales, turnover between communities is mostly explained by heterogeneity in habitat (Kitching et al. 2013, Basham et al. 2018, Sreekar et al. 2020). Vertical stratification is increasingly recognised as one of the key ecological mechanisms in structuring species distributions and diversity patterns. Habitats with high vertical complexity, such as forests, often house more species than habitats with low structural complexity (Oliveira and Scheffers 2019). Vertical stratification of communities has been documented for a range of habitats, from deep ocean to tropical forest, and is largely driven by variation in abiotic conditions and resources (Venegas-Li et al. 2018, Sheehan et al. 2019, Jorda et al. 2020). For example, in pelagic ecosystems, distance from insolation at the water surface drives vertical stratification (Li et al. 2020), whereas in terrestrial ecosystems shifts in vegetation structure with height can be important (Jarron et al. 2020). Although species turnover in relation to horizontal distance has been examined at large spatial scales (Chesters et al. 2019), it is often considered to be negligible at small scales, and therefore has rarely been incorporated into studies of vertical stratification (Roisin et al. 2006, Weiss et al. 2016). However, in complex ecosystems with high three-dimensional structural heterogeneity, such as coral reefs and tropical rain forests, abiotic and biotic factors can vary greatly at small horizontal and vertical scales (Reaka-Kudla 1997), which may drive small scale variation in community composition (Davies and Asner 2014). Although numerous studies have investigated how species diversity changes with horizontal and vertical distance, few have assessed both dimensions simultaneously at comparable spatial scales (Wermelinger et al. 2007). Tropical rain forest is one of the most structurally complex and biologically diverse habitats on earth (Ehrlich and Wilson 1991). In this habitat, the heterogenous environment from the ground to the canopy generates high microclimatic and structural complexity (Scheffers et al. 2013, Nakamura et al. 2017). First, microclimate, including air temperature, humidity and light intensity, can vary significantly along both vertical and horizontal dimensions and shape community composition through environmental filtering (Parker 1995, Scheffers et al. 2017). With increasing height, air temperature tends to monotonically increase while relative humidity tends to monotonically decrease due to the interplay between solar radiation and canopy buffering (Scheffers et al. 2013). Horizontally, microclimate can vary between open and shaded areas such as forest gaps and closed canopy forest (Fetcher et al. 1985, Parker 1995, Scheffers et al. 2017), although any monotonic changes clearly cannot persist over longer distances. For example, maximum air temperature can vary by as much as 2.2°C between the ground and 20 m above the forest floor in the canopy (Scheffers et al. 2013), while differences in maximum air temperature between shaded areas and forest gaps can exceed 8°C (Brown 1993; Kaspari et al., 2015; Stark et al. 2017). Second, influenced by the changes in abiotic conditions, various nutrient resources are distributed unevenly from ground to the canopy (Davidson 1997, Malhi et al. 2011), which may also influence community composition. Species distributions can be limited by key resources, such as food, habitat and supporting vegetation structure including tree size and leaf area (Dáttilo et al. 2014, Klimes 2017, Plowman et al. 2019). Finally, microhabitat connectivity

can also play an important role in shaping community composition in rain forest (Ramette and Tiedje 2007, Adams et al. 2019). Physical structures such as lianas, can form links along which organisms can travel (Bélisle 2005, Adams et al. 2017), when horizontal gaps in the canopy would otherwise isolate them, leading to high horizontal turnover in community composition (Adams et al. 2017, Adams et al. 2019). For non-flying arboreal organisms with limited ability to move, vertical movement is likely to be easier than horizontal movement when connectivity between trees is low (Adams et al. 2017). In addition, the interaction between resource availability and connectivity can also influence the importance of competition in driving species turnover (Matthiessen et al. 2010, Parr and Gibb 2010). Of the few studies considering variation in composition in both horizontal and vertical dimensions in tropical rain forest, patterns documented are idiosyncratic and tend to be taxon-dependent (Basham et al. 2018, Antoniazzi et al. 2021). The relevant scale when investigating spatial patterns of beta diversity can be dependent on the behavioural, morphological and physiological traits of the study organism and the variation in the habitat (Soininen et al. 2018). For amphibians in Madagascar, distance-decay was only found in the canopy and understory but not on the ground, which may be explained by limited habitat connectivity in the canopy (Basham et al. 2018). Conversely, distance-decay has been detected only in ground assemblages but not in canopy assemblages for ants in secondary forest in Mexico, which may relate to the higher dispersal capacity and larger territories of canopy ants, as well as higher microhabitat heterogeneity at the ground level (Antoniazzi et al. 2021). Nevertheless, how beta diversity of rain forest fauna changes at comparable horizontal and vertical distances remains largely unknown (Dial et al. 2004a, Nakamura et al. 2017), partly due to the technical challenges in conducting sampling across replicated horizontal positions for a range of vertical heights (Dial et al. 2004a).

Tropical arboreal ants are abundant and ecologically important, and are therefore an ideal study system to examine vertical and horizontal turnover in tropical forest (Yusah et al. 2018). The distribution and activity of ants in tropical forests are sensitive to microclimate variation (Kaspari 1993, Perfecto and Vandermeer 1996). The key resources ants rely on change with height in the canopy (Kaspari and Yanoviak 2001), and hence environmental filtering is expected to be important in determining ant community turnover. Furthermore, movement of flightless worker ants are likely limited by canopy connectivity (Adams et al. 2019). A large-scale experiment has demonstrated that the species richness, composition, and beta diversity of ants significantly changes after lianas, which provide both connectivity and nesting resources for arboreal ants, are removed (Adams et al. 2019).

Using traverse techniques, we surveyed arboreal ants at small spatial scale from the ground to the canopy at different horizontal positions in tropical rain forest in Sabah, Malaysia, which is home to both the world's tallest tropical trees and extremely high arthropod biodiversity (Shenkin et al. 2019). We tested how pairwise dissimilarity of ant assemblages across different vertical and horizontal positions related to spatial distance, microclimate and microhabitat structure. Specifically, we test two hypotheses that are not necessarily mutually exclusive (Fig. 1):

Environmental filtering will generate turnover of ant species (and therefore beta diversity) at small scales due to changes in microclimate and canopy structure. This will occur both vertically (e.g. ground-to-canopy temperature gradients) and horizontally (e.g. open vs closed areas temperature differences).

Habitat heterogeneity (connectivity) will create greater horizontal turnover of assemblages (and therefore beta diversity) than vertical turnover at small scale, as vertical tree architecture (trunks) provides connectivity for crawling ant workers.

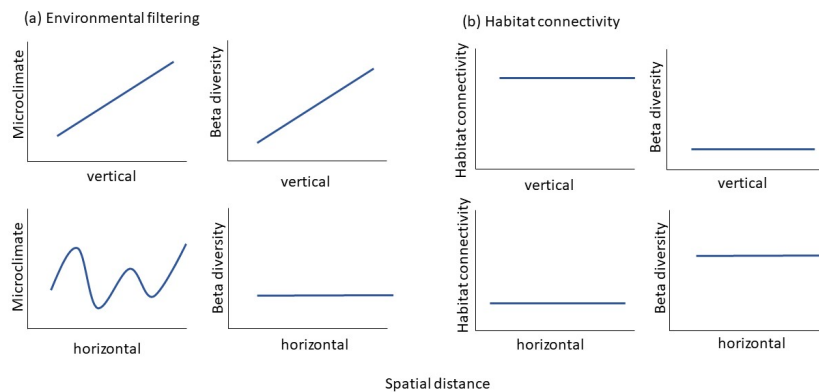


Figure 1. Predictions of how ant diversity could be influenced by environmental filtering and habitat connectivity. (a) The scenario in which environmental filtering is the dominant driver shaping beta diversity of ant assemblages across vertical and horizontal dimensions. In the vertical dimension, microclimate tends to change linearly with vertical height, and such changes are predicted to result in a linear relationship between vertical distance and beta diversity. In contrast, microclimate can vary non-linearly across horizontal space, in which case there should be no relationship between distance and beta diversity. (b) The scenario when habitat connectivity is the dominant factor in shaping beta diversity of ants across horizontal and vertical dimensions. Vertically, the habitat connectivity is high regardless of vertical distance, thus there is no effect of vertical distance on beta diversity, which remains low. Horizontally, habitat connectivity is likely to be low across trees and remain low across all distances, resulting in a lack of relationship between horizontal distance and beta diversity. However, due to lower habitat connectivity horizontally than vertically at comparable distances, the beta diversity of ants should be higher horizontally than vertically.

2 Materials and Methods

2.1 Study area

We conducted field sampling during April and May 2002 in primary lowland dipterocarp rain forest, part of a Class I forest reserve gazettement for Ulu Segama, near Danum Valley Field Centre, Sabah, Malaysian Borneo (4°57'N, 117°48'E) (Dial et al. 2004b; Dial et al. 2006) (Fig. 2). Mean temperature is 26.7°C ± 1.9°C, relative humidity ranges from 72%-100% (saturation) daily and mean annual rainfall is 2,669 mm (range: 1,918 - 3,294 mm) (Walsh and Newbery 1999). Rainfall is high in May-June and October-January, and is low in March-April and August-September (Walsh and Newbery 1999).

Our sampling was conducted over a 160 m × 70 m (vertical section) primary forest plot 150 m a.s.l., spanning a small tributary stream of the Segama River (Fig. 2). The ground was relatively level within the plot, without steep hillsides or ridges (Dial et al. 2004a). There were 11 trees from four families with canopies in contact with the transect, with nine individuals in the Dipterocarpaceae and Fabaceae families. These trees ranged from 40.8 m to 75.0 m in height (see Table S1 for details of tree species) and stood over an overstory of unidentified trees.

2.2 Field site

The field survey consisted of several activities. First, we established the vertical sampling system in April 2002 via a 200 m long application of “canopy trekking” to access the forest trees to secure a horizontal traverse line (Dial et al. 2004a). Once the 130 m traverse line was secured near the top of the three tallest trees, each > 65 m above ground level, we suspended seven vertical transects (Fig. 2). We used these vertical

transects to sample the canopy interior systematically from 1 m above ground to the traverse line 55-65 m above ground. Finally, we collected instantaneous measures of photosynthetically active radiation with a handheld meter, temperature and humidity with suspended data logging sensors, and fogging samples in May 2002 (Dial et al. 2006).

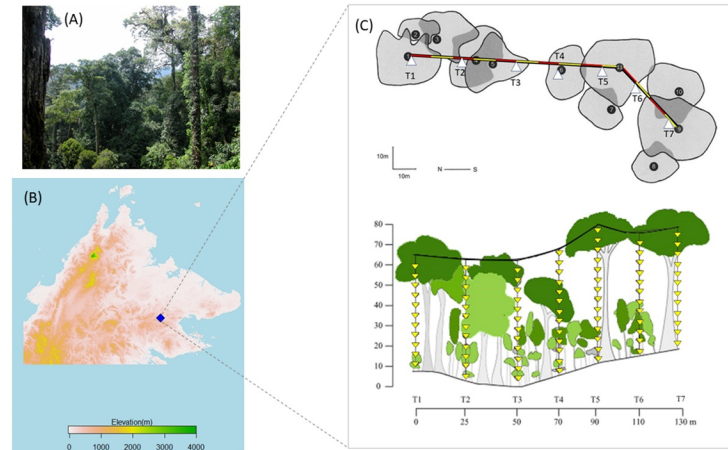


Figure 2. Study site and design: A) habitat photo of the sampling plot; B) Map of Sabah with elevation gradient presented (metres above sea level); C) The top and side view of the transect established within the forest plot (modified from Dial et al. 2004a and Dial et al. 2006).

Quantifying ant assemblages

Ant assemblages were sampled using insecticide fogging between 0700 and 0930 on 12-24 May 2002 from within the canopy by a climber rappelling down using a Swing-Fog model SN50 (Phoenix Fogger, Dallas, TX, USA) near each of seven vertical sample transects. These vertical transects were suspended from a 130 m horizontal traverse line secured in the upper canopy and were arranged at 20-25 m intervals horizontally (Fig. 2). Each of these transects supported multiple individual circular fogging trays (1 m²) (n=86) suspended in the air with attached ethanol-filled collecting bottles spaced at approximately 5 m vertical intervals beginning 1 m above the ground (Fig. 2). These trays collected knocked-down arthropods that were between trays at the time of fogging. A 1.6% aqueous solution of the synthetic pyrethrum (Cypermethrin) was used. Arthropods were collected into 80% ethanol 1-2 hours after fogging, and ants were separated as part of arthropod ordinal sorting (see Dial et al. 2006 for results on ordinal arthropod assemblages). The ants sampled using fogging are mainly diurnal foraging species active during the sampling period (0700 to 0930), and therefore likely present a subset of the total local ant diversity.

All worker ants were identified to genus following Fayle et al (2014), with relevant updates for taxonomy changes (Ward et al. 2015, Borowiec 2016, Ward et al. 2016), and then separated into morphospecies. Where possible, species names were assigned using online image databases (www.antweb.org, www.antbase.net), published literature (Hung 1970, Dorow and Kohout 1995, Schödl 1998, Kohout, 2006a, 2006b) and the collections of TMF. Reproductive individuals were excluded from the data, since their presence does not indicate an established colony, mating flights can confound estimates of abundance, and they can be challenging to match with workers unless entire nest series are collected. Lone major workers were also excluded for the latter reason. While all sample trays were suspended in the air at systematic, standardized horizontal and vertical positions, some trays captured no worker ants because there was only empty space with no foliage or stems between the sample tray without worker ants and the next sample tray above. In total, we obtained and identified ant assemblage samples for 61 out of 86 sampling points, with 14 samples having no ants, 9 samples having been lost between sampling and analysis, 2 samples in Transect 5 (two individuals of

ants discovered) belong to an emergent forest layer with no other horizontal positions to compare with.

2.2.2 Microclimate and microhabitat structure

To quantify microclimate and habitat structure, the air temperature (@C) and relative humidity (%) were measured at 0.5 h intervals over 24 hours using Hobo Pro RH/Temperature Data Logger (Onset Computer Corporation, Pocasset, MA, USA) during our sampling period. Data loggers were placed at 3 m intervals along each vertical transect, starting 1 m above the ground. At each sampling point, the photosynthetic photon flux density (PPFD) was recorded using a handheld light meter (Quantum Lightmeter, Spectrum Technologies, Plainfield, IL, USA), and was further normalized by dividing by maximum light value within each vertical transect to account for between-day variation in lighting; the intent was to identify the relative (not absolute) light environment of the forest canopy (Dial et al 2006). As microclimate was only measured over a single 24-hour period for each transect, the dataset does not capture daily microclimate variation at any single vertical transect, but rather reflects the spatial variation in microclimate across the vertical plane sampled. Although we measured microclimate over a relatively short time, the daily variation and vertical pattern in air temperature and relative humidity presented was consistent with microclimate patterns from a nearby lowland primary forest site over a longer time period (128 consecutive days measure in Maliau Basin Conservation Area (4@49'N, 116@54'E), Hardwick et al. 2015).

We estimated one-sided total leaf area between sampling trays as a measure of microhabitat structure at different sampling points for transects 1 to 6 (T1-T6; Fig 2c). The leaf area within a sampling interval was calculated by multiplying the number of leaf intersections by the size of the base area of the interval which was 1 m² (the area of the sample tray). We then used these data to estimate leaf area index (LAI) over vertical intervals (sampling methods described in Dial et al. 2004, 2006, and 2011; estimation methods in Dial et al. 2006 and 2011). Conceptually, LAI refers to the number of leaf layers above the ground surface that would be pierced by a vertical line. For example, if LAI = 7, then there are, on average seven leaf layers above a random point on the ground within that height range; or 7 m² of leaf area per m² of ground surface. We assumed (following MacArthur and Horn 1969) that at any sample point in the canopy located at height z above the ground, the foliage density was approximately equal in all directions. Following this assumption at each height z , we systematically measured horizontal distances (d_i) with a laser range finder to the nearest canopy element (foliage and stems) in 12 uniformly distributed azimuths every 2 m vertically from the ground to the height of the horizontal traverse line supporting the vertical transect. Using the n [?] 12 distances to foliage at each sample point, we found the mean distance (d) to foliage, doubled the mean (assuming that the observer was on average midway between foliage elements), then inverted it to find leaf intersections per vertical meter at height z as $LAI_z = 1/(2d)$. By multiplying the LAI_z by collection area (1m²) we estimated the leaf area sampled within the interval.

Data analyses All statistical analyses were conducted in R version 4.0.0 (R Core Team, 2013)

2.3.1 Assessing patterns in microclimate and microhabitat structure

We quantified microclimate (air temperature, relative humidity and PPFD) as well as changes in microhabitat structure (total leaf area) along both vertical and horizontal gradients. To be consistent with the assemblage data, we calculated the mean air temperature and relative humidity at the same scale (5 m vertical intervals) at which the ants were sampled by either using the data close to the 5 m interval point or using the average between sampling points. We expect microclimate and microhabitat structure to change directionally along vertical gradients due to canopy buffering effects, but to vary in a non-directional manner horizontally. As such, we ran separately four linear regression models for air temperature, relative humidity, PPFD and leaf area, with vertical height above ground as a continuous explanatory variable and horizontal position of vertical transects as a categorical explanatory variable.

2.3.2 Distribution of ant assemblages along vertical and horizontal gradients

To understand how ant richness and abundance changed vertically and horizontally, we used linear regression models. The abundance ($\ln(x+1)$ transformed) and richness of ants at each sampling point were used as

response variables with vertical height as a continuous explanatory variable and horizontal position of vertical transects as a categorical explanatory variable.

To explore vertical and horizontal differences in assemblage composition, we used NMDS ordinations. These used both abundance-based ($\ln(x+1)$ transformed) assemblage data and species presence/absence data. We generated non-metric multi-dimensional scaling (NMDS) plots using Bray-Curtis distance index for the abundance-based community and Jaccard distance index for the presence/absence data of ant assemblages at each sampling point grouped by vertical level and transect. For all ant assemblage composition analyses (NMDS and MRMs, see below), as results from measures using abundance-based and presence-absence based dissimilarity were similar, we only present results using abundance-based dissimilarity in the main text (see supplementary materials for results of presence-absence analyses). To increase the sample size within groups for the vertical analyses, and hence to increase statistical power, we assigned all sampling points within ten-metre bins to the same groups (i.e. 0-10 m, 10-20 m, etc). We tested for differences in assemblage composition between these groupings using PERMANOVA analyses (*adonis* function in the *vegan* package, 999 permutations) (Oksanen et.al. 2013, R Core Team, 2013).

To explore relationships between beta diversity and spatial distance we conducted multiple regressions on distance matrices (MRMs). We conducted two different analyses: one looking at beta diversity horizontally by summing assemblage data from entire transects across all heights, and a second looking at beta diversity vertically by summing assemblage data across all assemblages of the same height between different transects. We then calculated the pairwise assemblage dissimilarity across these summed data using the *beta.pair.abund* function (for abundance-based dissimilarity) and *beta.pair* function (for presence-absence data) in the *betapart* package (Baselga and Orme 2012). We then tested effects of horizontal/vertical distance on pairwise assemblage dissimilarity between transects/strata by conducting multiple regressions on these distance matrices (*MRM* function in R *ecodist* package) (Golsee and Urban 2007). To test whether degree of turnover differed horizontally and vertically, we conducted replicated MRM analysis using data from individual transects (to assess vertical turnover), and from individual heights (to assess horizontal turnover). We then took the slopes and intercepts from the fitted MRMs, and used linear models (function *lm* in R base package) to test for differences in these parameters horizontally and vertically. Slopes represent the strength of the distance-similarity decay relationship, with a more positive slope indicating a more rapid increase in dissimilarity. Intercepts represent the turnover at very small spatial scales (technically when distance = 0 m).

2.3.3 Correlates of habitat factors and ant assemblage composition

We conducted constrained ordinations to understand how microclimate (air temperature relative humidity, and PPFD) and microhabitat structure (total leaf area) affect ant assemblage composition. We first conducted Detrended Correspondence Analysis (DCA) using the *decorana* function in the *vegan* package and found maximum axis length greater than 4 (range: 3.91-6.96) indicating that Canonical Correspondence Analysis (CCA) constrained ordinations that assume unimodal responses of species to environmental gradients were appropriate. We then checked the collinearity among all explanatory variables using *vif.cca* function to reduce redundancy in the model. No strong collinearity ($VIF < 10$) was detected between microclimate and microhabitat variables, and so all predictors were included in the Canonical Correspondence Analysis (CCA). We then conducted CCA ordinations using *cca* function in the *vegan* package with all explanatory variables (air temperature, relative humidity, and PPFD). We conducted backward model selection using the *ordistep* function in the *vegan* package to identify the most significant variables affecting the assemblage composition based on permutation tests using 1000 permutations (Blanchet et al. 2008). As the model selection process for CCA analysis requires samples with all environmental factors available, only 48 out of total 61 ant assemblages that had all environmental information available were included for this analysis.

Results

3.1 Patterns of microclimate and microhabitat structure

We found high horizontal and vertical variation in microclimate (air temperature: $R^2 = 0.91$, $F_{7, 78} = 106.90$,

$P < 0.001$; relative humidity: $R^2 = 0.89$, $F_{7, 77} = 90.17$, $P < 0.001$) and microhabitat structure in our study site (Fig. 3). For every 10 m moved away from the forest floor, temperature increased by 0.13°C and relative humidity decreased by 1.4% (Fig. 3; Table S2). In addition, there was variation between horizontal locations in temperature (0.36 °C per 10 m) and humidity (1.4% per 10 m) (Table S2). Photosynthetic photon flux density (PPFD) increased with vertical height (as PPFD was normalized within each vertical transect, we could not compare this across transects, note that PPFD data was missing for Transect 7; $R^2 = 0.39$, $F_{1, 68} = 43.34$, $P < 0.001$; Table S2, Fig. 3). The total leaf area generally decreased towards the upper canopy but did not show significant horizontal variation (note that leaf area data was missing for Transect 7; $R^2 = 0.24$, $F_{6, 67} = 3.53$, $P = 0.004$; Table S2, Fig. 3).

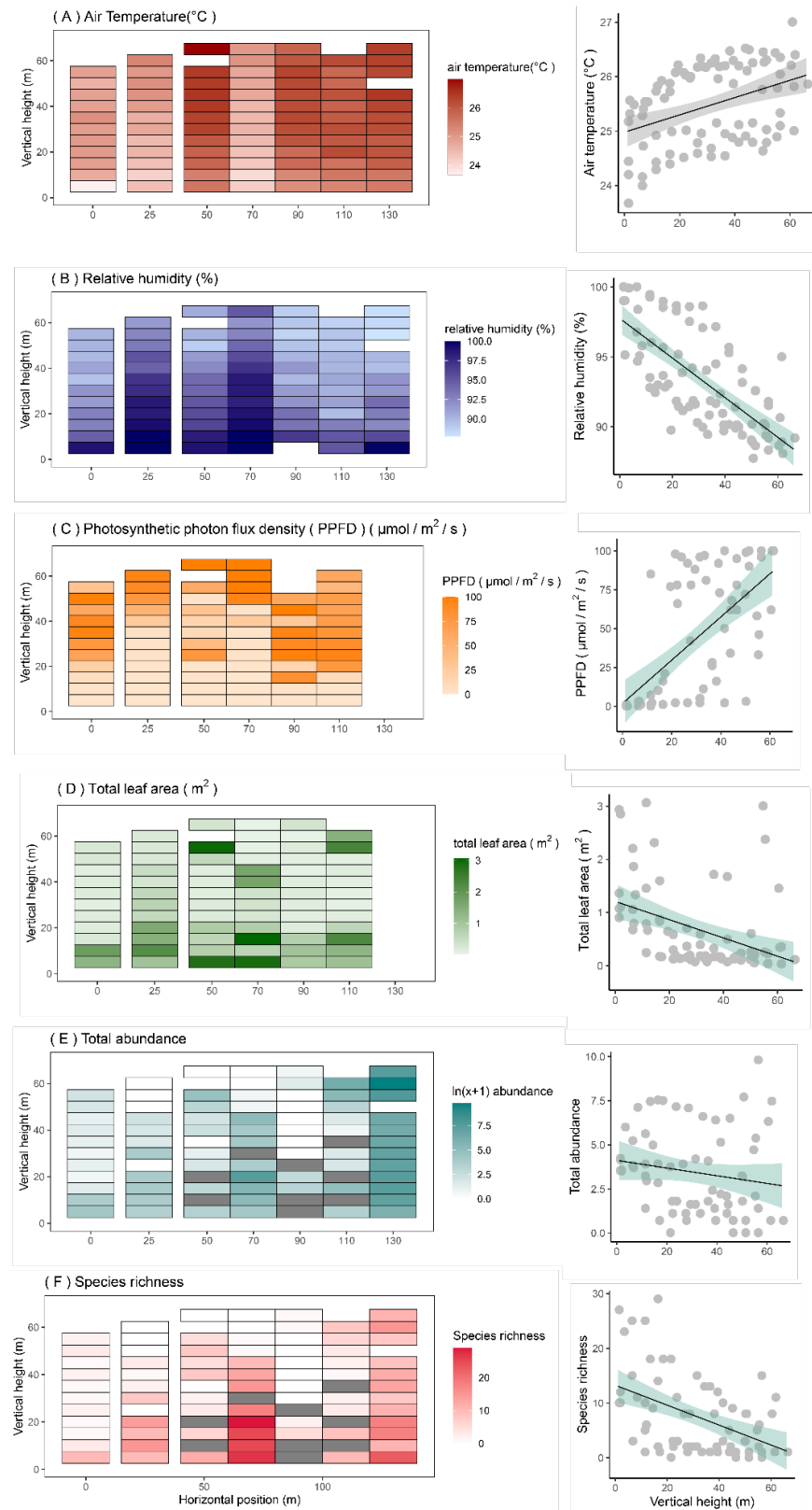


Figure 3. Heatmaps and scatter plots showing the horizontal and vertical distributions of (A) air temperature, (B) relative humidity, (C) photosynthetic photon flux density (PPFD), (D) total leaf area, (E) ant species abundance ($\ln(x+1)$ transformed), and (F) ant species richness. Colors with higher saturation indicate higher values of the variables. Plots with missing ant samples were highlighted by grey color in (E) and (F).

Distribution of ant assemblages along vertical and horizontal gradients

In total, 35,710 individual ants from 138 species in 31 genera were sampled. Ant abundance decreased significantly with increasing height in the canopy ($\ln(x+1)$ transformed, $R^2 = 0.67$, $F_{7, 59} = 16.68$, $P < 0.001$) from an average of 395 individuals per m^2 at 5 m, to 101 individuals per m^2 at 60 m. Ant species richness also significantly decreased with height in the canopy ($R^2 = 0.66$, $F_{7, 59} = 16.65$, $P < 0.001$), from an average of 12 species per m^2 at 5 m to an average of 3 species per m^2 at 60 m. Both ant abundance and richness also significantly varied across transects (horizontal positions) (Table S3, Fig. 3). Ant community assemblages showed significant differences in species composition both vertically and horizontally (Fig. S1 and S2; PERMANOVA analysis, vertical stratification: $F = 1.8$, $P = 0.01$, $R^2 = 0.09$; across transects: $F = 6.4$, $P = 0.001$, $R^2 = 0.39$).

We pooled data within the same transect or vertical stratum to examine distance-decay patterns between transects/strata. This showed strong effects of vertical distance on pairwise dissimilarity indexes between vertical strata (MRM analyses: coefficient = 0.007, $P = 0.001$, $R^2 = 0.65$, Fig. 4). In contrast, we found no effects of horizontal distance on pairwise assemblage dissimilarity between transects (MRM analyses: coefficient = 0.0003, $P = 0.52$, $R^2 = 0.02$, Fig. 4). At distances of < 50 m vertically and horizontally, pairwise dissimilarity was consistently higher horizontally than vertically (Fig. 4).

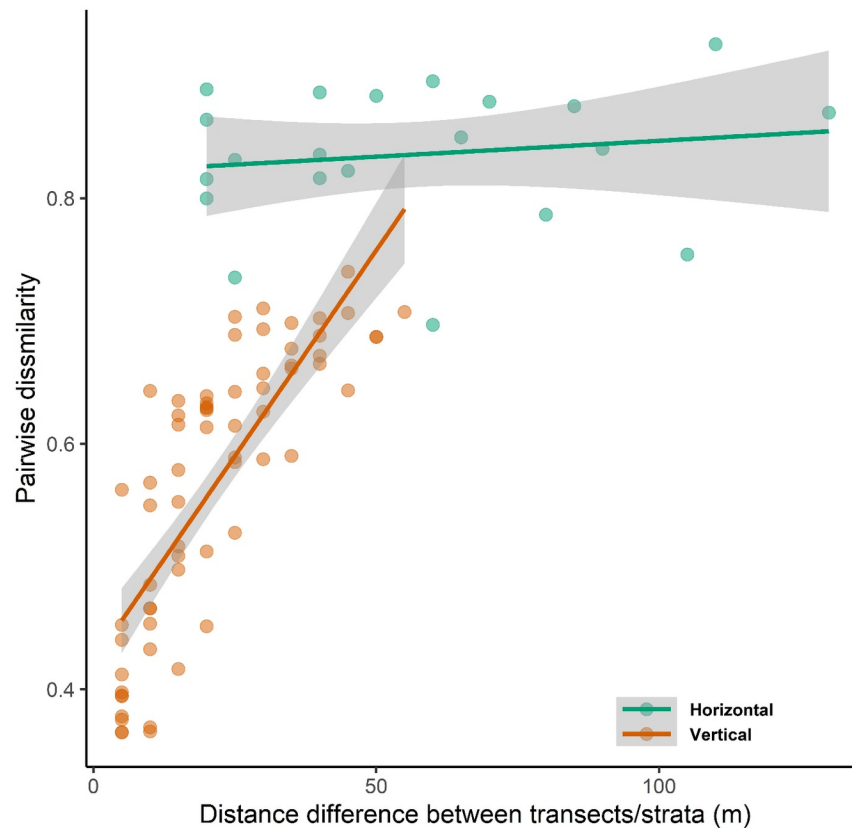


Figure 4. Effects of horizontal and vertical distance on abundance based pairwise dissimilarity of ant assem-

blages. Grey bands show 95% confidence intervals. Dissimilarity close to one indicates that two assemblages are highly different, while dissimilarity close to zero indicates that they are very similar.

By comparing the effects of vertical distance on assemblage dissimilarity within vertical transect and effects of horizontal distance within vertical strata, we found greater small-scale pairwise dissimilarity (higher intercepts) over horizontal distance within the same vertical strata than over vertical distance within the same vertical transect (linear regression: $F_{1, 17} = 25.93$, $P < 0.001$, $R^2 = 0.60$, Table S4, Fig. 5A). However, the effects of vertical distance on pairwise dissimilarity was much stronger than that of horizontal distance, presenting a distance-decay pattern within each transect (linear regression: $F_{1, 17} = 46.45$, $P < 0.001$, $R^2 = 0.73$, Table S4, Fig. 5B).

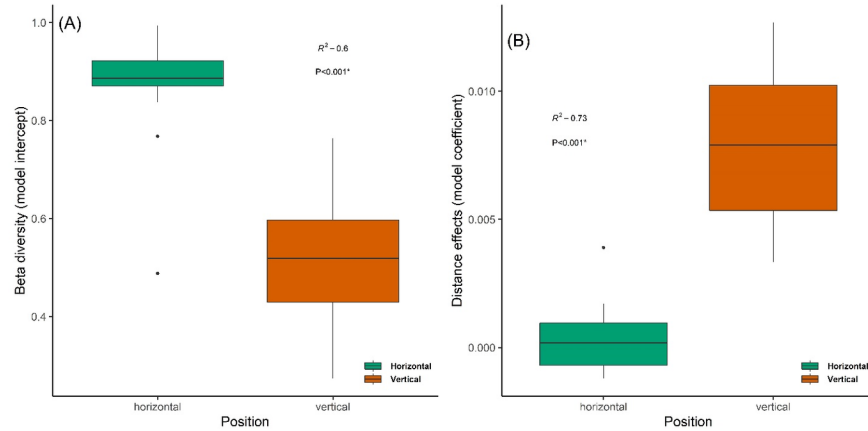


Figure 5. Boxplot showing the median and interquartile ranges (IQR) of the estimated very small scale beta diversity (model intercept) and distance effects (model coefficient) on pairwise dissimilarity between sampling points within transects/strata. Model intercepts and coefficients are from the linear regressions between distance and assemblage dissimilarity within each horizontal transect and vertical stratum (see Fig. S3 and Fig. S4). Whiskers denote $1.5 * \text{IQR}$. Data beyond this range are plotted individually.

3.3 Correlates of ant assemblage composition

Results from Canonical Correspondence Analysis (CCA) backward model selection indicated that both air temperature and relative humidity were significantly associated with ant assemblage composition, while PPFD and total leaf area did not show significant effects (Fig. 6, Table S5).

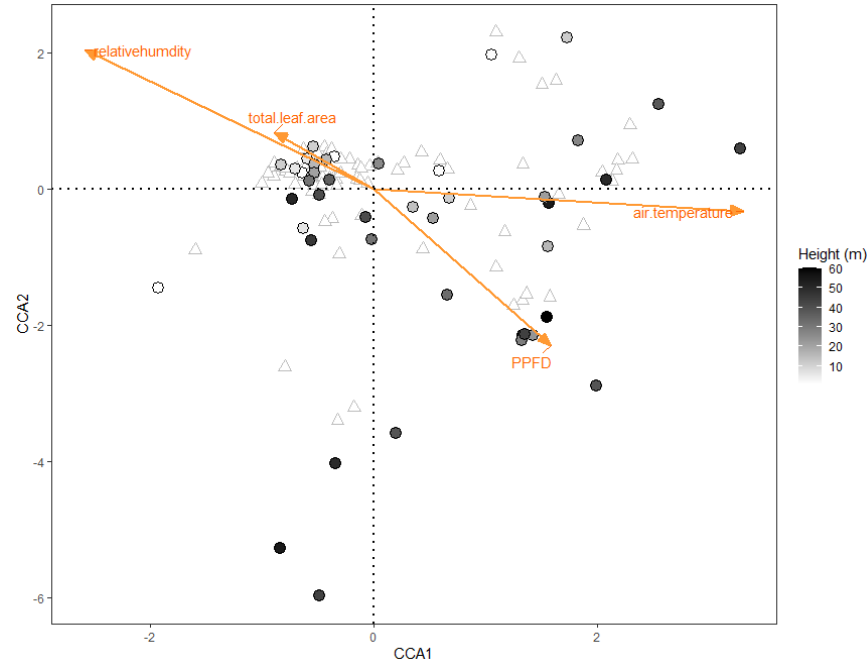


Figure 6 Canonical correspondence analysis (CCA) of ant community composition explained by effects of microclimate (air temperature, relative humidity, and photosynthetic photon flux density (PPFD)) and vegetation profile (total leaf area). Circle points represent different sampling location, darker color indicates higher vertical position. Triangles represent ant species.

4. Discussion

We observed different patterns in species assemblage distribution over small-scale vertical and horizontal gradients in a complex habitat. The high local diversity of arboreal ants can be explained by high environmental and habitat heterogeneity along both horizontal and vertical dimensions. We found consistently greater horizontal turnover in ant assemblages than that observed at comparable vertical distances. However, a distance-decay pattern of ant turnover was only detected vertically, but not horizontally, with the high species turnover between horizontal positions being independent of distance. The observed patterns confirmed our hypotheses, and are likely associated with continuous directional changes in environment (i.e., microclimate) and resources vertically, and stochastic variation in environment and resources, as well as poor connectivity horizontally.

We found the spatial distribution of ant assemblages was associated with heterogeneity in air temperature and relative humidity within the three-dimensional structure of the forest. The spatial pattern of microclimate variables in our study plot is in line with other studies in tropical rain forest: air temperature increased with height above ground, while relative humidity decreased (Davis et al. 2019, De Frenne et al. 2019). Horizontal variation in microclimate was also high but without directional change, presumably relating to variation in vegetation structure within and between trees (Fetcher et al. 1985, Scheffers et al. 2017). Such non-directional horizontal variation in microclimate may contribute to the high turnover of ant assemblages and lack of distance-decay pattern in this dimension at the scales we sampled. Given that turnover at very short horizontal distances was already nearly maximal, it would not have been possible for turnover to then be even greater with increasing horizontal distance. Tropical arboreal ants show thermal adaptation to their vertical habitat use through their physiology (Kaspari et al. 2015), morphology (Law et al. 2020) and nesting site selection (Plowman et al. 2019). The high variance in microclimate generates diverse thermal niches for ant species with different thermal tolerances, and hence can facilitate co-existence of multiple species at small

spatial scales (Lessard et al. 2009). For tiny ectotherms like ants, fine-scale environmental heterogeneity can play an important role in defining their distributions, probably due to the small foraging range and small body size of ants, and the thermal diversity of the environment (Ribas and Schoereder 2007, Fayle et al. 2010, Klimes et al. 2012, Kaspari et al. 2015, Bütikofer et al. 2020). The association between microclimate pattern and ant assemblage composition may result not only from direct effects through environmental preferences of ant species, but can also be a consequence of indirect biotic effects, for example if microclimate influences ant food availability. However, the relative importance of direct and indirect microclimate influences on ant assemblage composition remains to be investigated.

In addition to microclimate, biotic influences such as resource limitation and vegetation structure may also contribute to the high horizontal turnover we observed. The decline in ant richness and abundance with height in the canopy could be due to reduction in leaf area, which limits foraging range and nest site availability (Adams et al. 2019, Plowman et al. 2019). Ant assemblage composition can be affected by vegetation structure such as tree size, number of branches, and cavity diversity (Powell et al. 2011, Yusah and Foster 2016, Adams et al. 2019, Plowman et al. 2019). Hence, we can expect distinct ant communities to be hosted by different individual trees and that the distance between trees per se might not be driving assemblage dissimilarity. The lack of distance effects on high horizontal turnover arboreal ants in our study is consistent with that found in canopy ant assemblages across greater horizontal distances (100-700 m) in Mexican rain forest, whereas a distance-decay pattern was observed in ground ant assemblages (Antoniazzi et al. 2021). For social insects like ants where workers are wingless, vertical movement of workers within the colony tree is likely to be less challenging than movement between trees, especially without vegetation connections such as lianas (Yusah and Foster 2016, Adams et al. 2019), which may be less common in the Asian tropics compared with the American tropics (Dial et al. 2004a). Such lack of connectivity between individual trees means that each tree canopy might function as an island within the forest (Southwood and Kennedy 1983, Adams et al. 2017).

Our findings offer important insights into the way in which biodiversity is maintained at fine scales in complex three-dimensional habitats. The high species richness discovered within the 130 m long by 70 m high vertical plot in our study site represents a high proportion of ant diversity at larger scales. The number of species that we detected using precision fogging across vertical strata among 11 trees reached about 40% of the number of species sampled in a similar forest habitat elsewhere in Sabah from 99 trees (Floren et al. 2014). This finding of a relatively large proportion of regional biodiversity being sampled from small plots within rain forest is in line with patterns for herbivorous insects (Novotny et al. 2007), birds (Huang and Catterall 2021) and butterflies (Daily and Ehrlich 1995) and is likely driven by high structural complexity at small scales (Basset et al. 2012).

Our findings need to be interpreted with the caveats of our limited sampling time and sample size. Microclimate information was only monitored for 24 hours for each transect, although we feel that this is representative of longer-term patterns (see above). Future studies involving long term monitoring of microclimate at fine spatial scales are needed to understand the distribution of microclimate with the complex three-dimensional structure of tropical rain forest. In addition, although our sampling intensity per tree was high, we sampled across a relatively limited spatial area and some samples were missing. Future research using greater numbers of replicates at larger spatial scales are needed to confirm the generality pattern we report here.

5. Conclusion

Our study reveals high spatial variation in ant communities in both horizontal and vertical dimensions over small spatial scales. We detected a distance-decay pattern in ant assemblage composition across vertical forest strata, but no effects of horizontal distance on assemblage turnover across trees. We also found higher horizontal turnover in ant assemblages than vertical turnover at short spatial scales. These patterns are associated with variation in air temperature and relative humidity. Connectivity may also play a role in driving the high turnover of ant assemblages horizontally. Our findings highlight the necessity of considering species turnover in multiple spatial dimensions, and furthermore reveal the importance of microhabitat complexity

in maintaining high biodiversity in tropical forest. Such insights will be vital for future preservation of the biodiversity of highly diverse tropical forests under anthropogenic global change impacts.

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Data Availability Statement

We agree to archive all the data associated with the manuscript to DRYAD (<https://datadryad.org/stash>) should this paper be accepted. We are thankful to Mr Runxi Wang for his help in figure design, analysis and comments on the draft of the study.

References

- Adams, B. J., Schnitzer, S. A., and Yanoviak, S. P. 2017. Trees as islands: canopy ant species richness increases with the size of liana-free trees in a Neotropical forest. *Ecography* **40** : 1067–1075.
- Adams, B. J., Schnitzer, S. A., and Yanoviak, S. P. 2019. Connectivity explains local ant community structure in a Neotropical forest canopy: a large-scale experimental approach. *Ecology* **100** : e02673.
- Antoniazzi, R., Viana-Junior, A. B., Pelayo-Martinez, J., Ortiz-Lozada, L., Neves, F. S., Leponce, M., and Dattilo, W. 2021. Distance–decay patterns differ between canopy and ground ant assemblages in a tropical rainforest. *J. Trop. Ecol.* 1–9.
- Ashton, L. A., Nakamura, A., Basset, Y., Burwell, C. J., Cao, M., Eastwood, R., ... Kitching, R. L. 2016. Vertical stratification of moths across elevation and latitude. *Journal of Biogeogr.***43**: 59–69.
- Baselga, A., and Orme, C. D. L. 2012. betapart: an R package for the study of beta diversity. *Methods ecol evol.* **3** : 808–812.
- Basham, E. W., Seidl, C. M., Andriamahohatra, L. R., Oliveira, B. F., and Scheffers, B. R. 2018. Distance–decay differs among vertical strata in a tropical rainforest. *J. Anim. Ecol* **88** : 114–124
- Basset, Y., Cizek, L., Cuenoud, P., Didham, R. K., Guilhaumon, F., Missa, O., ... Leponce, M. 2012. Arthropod diversity in a tropical forest. *Science* . **338**: 1481–1484.
- Belisle, M. 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. *Ecology* **88**: 1988–1995.
- Blanchet, F. G., Legendre, P., and Borcard, D. 2008. Forward selection of explanatory variables. *Ecology* **89** : 2623–2632.
- Borowiec, M. L. 2016. Generic revision of the ant subfamily dorylinae (hymenoptera, formicidae). *ZooKeys* **608** : 1
- Brown, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *J Trop. Ecol.* 153–168.
- Butikofer, L., Anderson, K., Bebbler, D. P., Bennie, J. J., Early, R. I., and Maclean, I. M. D. 2020. The problem of scale in predicting biological responses to climate. *Glob. Chang. Biol.***26** : 6657–6666.
- Chesters, D., Beckschafer, P., Orr, M. C., Adamowicz, S. J., Chun, K. P., and Zhu, C. D. 2019. Climatic and vegetational drivers of insect beta diversity at the continental scale. *Ecol. Evol.* **9** : 13764–13775.
- Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecol Lett.* **8** : 1175–1182.

- Daily, G. C., and Ehrlich, P. R. 1995. Preservation of biodiversity in small rainforest patches: rapid evaluations using butterfly trapping. *Biodivers. Conserv.* **4** : 35-55
- Dattilo, W., Fagundes, R., Gurka, C. A., Silva, M. S., Vieira, M. C., Izzo, T. J., ... and Rico-Gray, V. 2014. Individual-based ant-plant networks: diurnal-nocturnal structure and species-area relationship. *PLoS One*. **9** : e99838.
- Davies, A. B., and Asner, G. P. 2014. Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends Ecol. Evol.***29** : 681–691.
- Davis, K. T., Dobrowski, S. Z., Holden, Z. A., Higuera, P. E., and Abatzoglou, J. T. 2019. Microclimatic buffering in forests of the future: the role of local water balance. *Ecography* , **42** : 1–11.
- Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.* **61** : 153-181.
- De Frenne, P., Zellweger, F., Rodriguez-Sanchez, F., Scheffers, B. R., Hylander, K., Luoto, M., ... Lenoir, J. 2019. Global buffering of temperatures under forest canopies. *Nature Ecol Evol.* **3** : 744–749.
- Dial, R., Bloodworth, B., Lee, A., Boyne, P. and Heys, J., 2004a. The distribution of free space and its relation to canopy composition at six forest sites. *Forest Science* **50** : 312-325.
- Dial, R. J., Sillett, S. C., Antoine, M. E., and Spickler, J. C. 2004b. Methods for horizontal movement through forest canopies. *Selbyana***25**:151-163.
- Dial, R. J., Ellwood, M. D. F., Turner, E. C., and Foster, W. A. 2006. Arthropod Abundance, Canopy Structure, and Microclimate in a Bornean Lowland Tropical Rain Forest. *Biotropica*. **38** : 643–652.
- Dial, R. J., Nadkarni, N. M., and Jewell III, C. D. 2011. Canopy structure in a 650-year Douglas-fir chronosequence in western Washington: Distribution of canopy elements and open space. *Forest Science* **57** : 309-319.
- Dorow, W.H., and Kohout, R.J. 1995. A review of the subgenus Hemioptica Roger of the genus *Polyrhachis* Fr. Smith with description of a new species (Hymenoptera: Formicidae: Formicinae). *Zoologische Mededelingen* . **69** : 93-104.
- Ehrlich, P. R., and Wilson, E. O. 1991. Biodiversity studies: Science and policy. *Science* , **253** : 758–762.
- Fayle, T. M., Turner, E. C., Snaddon, J. L., Chey, V. K., Chung, A. Y. C., Eggleton, P., and Foster, W. A. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic Appl Ecol.* **11** : 337-345.
- Fayle, T. M., Yusah, K. M., and Hashimoto, Y. 2014. Key to the ant genera of Borneo in English and Malay. <http://www.tomfayle.com/Ant%20key.htm>.
- Fetcher, N., Oberbauer, S. F., and Strain, B. R. 1985. Vegetation effects on microclimate in lowland tropical forest in Costa Rica.*Int. J. Biometeorol.* **29** : 145–155.
- Floren, A., Wetzels, W., and Staab, M. 2014. The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. *Myrmecol. News* **19** : 65-74.
- Goslee, S. C., and Urban, D. L. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.* **22**: 1-19.
- Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., and Ewers, R. M. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agric For Meteorol.* **201** : 187-195.
- Huang, G., and Catterall, C. P. 2021. Effects of habitat transitions on rainforest bird communities across an anthropogenic landscape mosaic.*Biotropica* . **53** : 130-141.

- Hung AC. 1970 A revision of ants of the subgenus *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae: Formicinae). *Orient. Insects*. **4** :1-36.
- Jarron, L. R., Coops, N. C., MacKenzie, W. H., Tompalski, P., & Dykstra, P. 2020. Detection of sub-canopy forest structure using airborne LiDAR. *Remote Sens. Environ.* **244** : 111770.
- Jorda, G., Marba, N., Bennett, S., Santana-Garcon, J., Agusti, S., and Duarte, C. M. 2020. Ocean warming compresses the three-dimensional habitat of marine life. *Nature Ecol. Evol.* **4** : 109–114.
- Kaspari, M. 1993. Body size and microclimate use in Neotropical granivorous ants. *Oecologia* . **96** : 500-507.
- Kaspari, M., Clay, N. A., Lucas, J., Yanoviak, S. P., and Kay, A. 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. *Global Change Biol.* **21** : 1092–1102.
- Kaspari, M., and Yanoviak, S. P. 2001. Bait Use in Tropical Litter and Canopy Ants—Evidence of Differences in Nutrient Limitation. *Biotropica* . **33** : 207-211.
- Klimes, P. 2017. Diversity and specificity of ant-plant interactions in canopy communities: insights from primary and secondary tropical forests in New Guinea. *Ant-Plant Interactions—Impacts of Humans on Terrestrial Ecosystems* , 26-51.
- Kitching, R. L., Ashton, L. A., Nakamura, A., Whitaker, T., and Khen, C. V. 2013. Distance-driven species turnover in Bornean rainforests: Homogeneity and heterogeneity in primary and post-logging forests. *Ecography* . **36** : 675-682.
- Kohout, R.J. 2006a. Review of *Polyrhachis* (Cyrtomyrma) Forel (Hymenoptera: Formicidae: Formicinae) of Australia, Borneo, New Guinea and the Solomon Islands with descriptions of new species. *Memoirs-Queensland Museum* , 52: 87.
- Kohout R.J. 2006b. A review of the *Polyrhachiscryptoceroideis* species-group with description of a new species from Thailand (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* .;8:145-50.
- Klimes, P., Idigel, C., Rimandai, M., Fayle, T. M., Janda, M., Weiblen, G. D., and Novotny, V. 2012. Why are there more arboreal ant species in primary than in secondary tropical forests? *J. Anim. Ecol.* **81** : 1103–1112.
- Law, S. J., Bishop, T. R., Eggleton, P., Griffiths, H., Ashton, L., and Parr, C. 2020. Darker ants dominate the canopy: Testing macroecological hypotheses for patterns in colour along a microclimatic gradient. *J. Anim. Ecol.* **89**: 347–359.
- Lessard, J. P., Dunn, R. R., and Sanders, N. J. 2009. Temperature-mediated coexistence in temperate forest ant communities. *Insectes Soc.* **56** : 149-156.
- Li, G., Cheng, L., Zhu, J., Trenberth, K. E., Mann, M. E., & Abraham, J. P. (2020). Increasing ocean stratification over the past half-century. *Nature Climate Change* **10** : 1116-1123.
- MacArthur, R. H., and Horn, H. S. 1969. Foliage profile by vertical measurements. *Ecology* . **50** : 802-804.
- Majer, J. D. 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia-its structure and influence on arthropod diversity. *Hymenoptera and Biodiversity*. 115-141.
- Malhi, Y., Doughty, C., and Galbraith, D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philos. Trans. R. Soc. B: Biol. Sci.* , **366** : 3225-3245.
- Matthiessen, B., Mielke, E., and Sommer, U. 2010. Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition. *Ecology*. **91** : 2022-2033.
- Nakamura, A., Kitching, R. L., Cao, M., Creedy, T. J., Fayle, T. M., Freiberg, M., ... Ashton, L. A. 2017. Forests and Their Canopies: Achievements and Horizons in Canopy Science. *Trends Ecol. Evol.* **32** : 438–451.

- Nekola, J. C., and McGill, B. J. 2014. Scale dependency in the functional form of the distance decay relationship. *Ecography* .**37** : 309–320.
- Novotny, V., Miller, S. E., Hulcr, J., Drew, R. A. I., Basset, Y., Janda, M., ... Weiblen, G. D. 2007. Low beta diversity of herbivorous insects in tropical forests. *Nature* **448** : 692–695.
- Oliveira, B. F., and Scheffers, B. R. 2019) Vertical stratification influences global patterns of biodiversity. *Ecography* .**42** : 249–249.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ... and Wagner, H. 2013. Community ecology package. *R package version* , 2-0.
- Parker, G. G. 1995. Structure and microclimate of forest canopies. In M.D. Lowman, and N. M. Nadkarni (Eds.), *Forest canopies* (pp. 73–106). SanDiego, CA: Academic Press Inc.
- Parr, C. L., and Gibb, H. 2010. Competition and the role of dominant ants. *Ant ecology* , 77–96.
- Perfecto, I., and Vandermeer, J. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. *Oecologia* , **108** : 577–582.
- Plowman, N. S., Mottl, O., Novotny, V., Idigel, C., Philip, F. J., Rimandai, M., and Klimes, P. 2019. Nest microhabitats and tree size mediate shifts in ant community structure across elevation in tropical rainforest canopies. *Ecography* . **43**: 431–442.
- Powell, S., Costa, A. N., Lopes, C. T., and Vasconcelos, H. L. 2011. Canopy connectivity and the availability of diverse nesting resources affect species coexistence in arboreal ants. *J. Anim. Ecol.***80** : 352–360
- R core team. 2013. R: A language and environment for statistical computing.
- Ramette, A., and Tiedje, J. M. 2007. Multiscale responses of microbial life to spatial distance and environmental heterogeneity in a patchy ecosystem. *Proc. Natl. Acad. Sci. U.S.A.* **104** :2761–2766.
- Reaka-Kudla, M.L. 1997. The Global Biodiversity of Coral Reefs: A Comparison with Rain Forests. *Biodiversity II: Understanding and Protecting Our Biological Resources* . Joseph Henry Press.
- Ribas, C. R., and Schoederer, J. H. 2007. Ant communities, environmental characteristics and their implications for conservation in the Brazilian Pantanal. *Biodivers. Conserv* . **16** : 1511–1520
- Roisin, Y., Dejean, A., Corbara, B., Orivel, J., Samaniego, M., and Leponce, M. 2006. Vertical stratification of the termite assemblage in a neotropical rainforest. *Oecologia* , **149** : 301–311.
- Sanders, N. J., Crutsinger, G. M., Dunn, R. R., Majer, J. D., and Delabie, J. H. 2007. An ant mosaic revisited: Dominant ant species disassemble arboreal ant communities but co-occur randomly. *Biotropica* , **39** : 422–427.
- Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R., Roslan, N., ... Williams, S. E. 2017. Extreme thermal heterogeneity in structurally complex tropical rain forests. *Biotropica* **49** : 35–44.
- Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A., and Williams, S. E. 2013. Increasing arboreality with altitude: A novel biogeographic dimension. *Proc. Royal Soc. B* ,**1770**: 20131581.
- Schodl, S. 1998. Taxonomic revision of Oriental Meranoplus F. Smith, 1853 (Insecta: Hymenoptera: Formicidae: Myrmicinae). *Annalen des Naturhistorischen Museums in Wien. Serie B fur Botanik und Zoologie*,361–394.
- Sheehan, T. N., Ulyshen, M. D., Horn, S., and Hoebeke, E. R. 2019. Vertical and horizontal distribution of bark and woodboring beetles by feeding guild: is there an optimal trap location for detection? *J. Pest. Science.* **92** : 327–341.

- Shenkin, A., Chandler, C. J., Boyd, D. S., Jackson, T., Disney, M., Majalap, N., ... Malhi, Y. 2019. The World's Tallest Tropical Tree in Three Dimensions. *Front. for. glob. change.* **2** : 32.
- Soininen, J., Heino, J., and Wang, J. 2018. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecol. Biogeogr.* **27** : 96–109.
- Southwood, T. R. E., and Kennedy, C. E. J. 1983. Trees as Islands. *Oikos* . 359-371
- Sreekar, R., Corlett, R. T., Dayananda, S., Goodale, U. M., Kilpatrick, A., Kotagama, S. W., ... and Goodale, E. 2017. Horizontal and vertical species turnover in tropical birds in habitats with differing land use. *Biol. Lett.* **13** : 20170186.
- Sreekar, R., Koh, L. P., Mammides, C., Corlett, R. T., Dayananda, S., Goodale, U. M., ... Goodale, E. 2020. Drivers of bird beta diversity in the Western Ghats–Sri Lanka biodiversity hotspot are scale dependent: roles of land use, climate, and distance. *Oecologia* .**193** : 801-809.
- Stark, A. Y., Adams, B. J., Fredley, J. L., & Yanoviak, S. P. (2017). Out on a limb: Thermal microenvironments in the tropical forest canopy and their relevance to ants. *J. Therm. Biol.* **69** , 32-38.
- Venegas-Li, R., Levin, N., Possingham, H., and Kark, S. 2018. 3D spatial conservation prioritisation: Accounting for depth in marine environments. *Methods. Ecol. Evol.* **9** : 773–784.
- Walsh, R. P. D., and Newbery, D. M. 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Proc. Royal Soc. B.***354** : 1869-1883
- Ward, P. S., Blaimer, B. B., and Fisher, B. L. 2016. A revised phylogenetic classification of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of the genera *Colobopsis* and *Dinomyrmex* . *Zootaxa* . **4072** : 343-357
- Ward, P. S., Brady, S. G., Fisher, B. L., and Schultz, T. R. 2015. The evolution of myrmicine ants: Phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Syst. Entomol.***40** : 61-81.
- Weiss, M., Prochazka, J., Schlaghamersky, J., and Cizek, L. 2016. Fine-Scale vertical stratification and guild composition of saproxylic beetles in lowland and montane forests: Similar patterns despite low faunal overlap. *PLoS ONE* . 11: e0149506.
- Wermelinger, B., Fluckiger, P. F., Obrist, M. K., and Duelli, P. 2007. Horizontal and vertical distribution of saproxylic beetles (Col., Buprestidae, Cerambycidae, Scolytinae) across sections of forest edges. *J. Appl. Entomol.* **131** : 104-114.
- Yusah, K. M., and Foster, W. A. 2016. Tree size and habitat complexity affect ant communities (Hymenoptera: Formicidae) in the high canopy of Bornean rain forest. *Myrmecol. News* **23** : 15-23.
- Yusah, K. M., Foster, W. A., Reynolds, G., and Fayle, T. M. 2018. Ant mosaics in Bornean primary rain forest high canopy depend on spatial scale, time of day, and sampling method. *PeerJ* . **6** : e4231.
- Zellweger, F., Roth, T., Bugmann, H., and Bollmann, K. 2017. Beta diversity of plants, birds and butterflies is closely associated with climate and habitat structure. *Global Ecol. Biogeogr.***26** : 898-906.