

Species assemblage turnover is greater horizontally than vertically in a complex habitat

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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 decreased resource availability in the upper canopy, environmental filtering by microclimate and microhabitat structure, presence of competition in the form of ant mosaics, and structural connectivity. We found although dissimilarity between ant assemblages increased with vertical distance, the dissimilarity was higher horizontally but was independent of distance in this dimension. Moreover, there was not a more rapid increase in horizontal distance-dissimilarity at greater heights in the canopy, as would be predicted if large competitive ant colonies drove these patterns. 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.

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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 decreased resource availability in the upper canopy, environmental filtering by microclimate and microhabitat structure, presence of competition in the form of ant mosaics, and structural connectivity. We found although dissimilarity between ant assemblages increased with vertical distance, the dissimilarity was higher horizontally but was independent of distance in this dimension. Moreover, there was not a more rapid increase in horizontal distance-dissimilarity at greater heights in the canopy, as would be predicted if large competitive ant colonies drove these patterns. 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 Variation in community composition in space is 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 large spatial scales, turnover between communities is generally driven by dispersal limitation and environmental filtering (i.e. the process where abiotic factors such as climatic gradients prevent species from establishing or persisting in a particular area) (Tuomisto et al. 2003, Qian and Ricklefs 2007, Sreekar et al. 2020). Whereas at small spatial scales, turnover between communities is mostly explained by heterogeneity in habitat, and distance effects can be less important (Kitching et al. 2013, Basham et al. 2018, Sreekar et al. 2020). In addition, biotic factors such as changes in resource availability and interspecific competition can also drive community turnover across multiple spatial scales (Zellweger et al. 2017). This turnover of ecological communities occurs in both vertical and horizontal dimensions (Sreekar et al. 2017). Vertical stratification generated by vegetation height is increasingly recognised as one of the key ecological mechanisms in structuring species distributions and diversity patterns at large spatial scales (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 structured by variation in abiotic conditions and resources (Venegas-Li et al. 2018, Sheehan et al. 2019, Jorda 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 cause short distance 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 a structurally complex habitat that supports most biologically diverse terrestrial habitat 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). Vertically, due to the interplay between the solar radiation and canopy buffering, air temperature tends to monotonically increase with vertical height while relative humidity tends to monotonically decrease with vertical height (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 height in the canopy (Scheffers et al. 2013), while the maximum air temperature variation between shaded areas and forest gaps can reach 8°C (Brown 1993). Second, influenced by the changes in abiotic conditions, various nutrient resources, including net primary productivity, carbohydrates and nitrogen, are distributed unevenly from ground to the canopy (Davidson 1997, Malhi et al. 2011), which may also influence the species distributions. Species distribution 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). If there is variation in only the amount of these resources, but not their composition, then this mechanism potentially only drives reductions in abundance and richness, but does not necessarily lead to changes in composition. 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 (e.g. vines) can form links along which organisms can travel (Bélisle 2005, Adams et al. 2017), and horizontal gaps in the canopy can isolate them, leading to high horizontal turnover in community composition (Adams et al. 2017, Adams et al. 2019). For non-flying arboreal ectotherms with limited mobile ability, it could be easier for them to move vertically rather than horizontally when there is lack of connectivity between trees (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 ground level (Antoniazzi et al. 2021). 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 therefore ideal to examine vertical and horizontal turnover in tropical forest (Yusah et al. 2018). The diversity distribution and activity of tropical ants are sensitive to microclimate variation in forest (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, flightless worker ants are likely limited by canopy connectivity (Adam 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 nest resource for arboreal ants, are removed (Adams et al. 2019). Moreover, “ant mosaic” patterns have been observed in canopy ants in many tropical forest sites, with segregation of numerically dominant and subdominant species that establish large colonies and territories (Majer 1993, Davidson et al. 2007, Sanders et al. 2007, Yusah et al. 2018, Dejean et al. 2019). If the territories of dominant ant species (and their species-specific subordinates) are large, then horizontal turnover is expected to be low at short distances in the upper canopy, but then become much greater at the distances which span multiple dominant territories. Conversely, in the lower canopy where the dominant ant species that form mosaics are less abundant, a slower increase in turnover with horizontal distances is predicted. As such, we may expect different horizontal distance-decay patterns from the ground to the canopy if there is strong “ant mosaic” effect on ant assemblage turnover in forest canopies.

Using traverse techniques, we surveyed arboreal ants at fine spatial scale from ground to the canopy at different horizontal positions in tropical rain forest in Sabah, Malaysia. Sabah is home to both the world’s tallest tropical trees and 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, microclima-

te and microhabitat structure. We further partition the dissimilarity into richness difference (nestedness) and replacement (turnover). Specifically, we test a series of hypotheses (that are not necessarily mutually exclusive):

1. Environmental filtering will generate turnover of ant species both vertically and horizontally and that as a result, this turnover will be correlated with variables important for ants, such as microclimate and canopy structure.
2. If connectivity is important, then horizontal turnover of assemblages should be greater than vertical turnover of assemblages at comparable spatial scales, since vertical tree architecture can provide connectivity for crawling ant workers.
3. Ant mosaics will result in rapid horizontal turnover as scale increases beyond that of the typical range of dominant or subdominant ant territory. This pattern is expected to be stronger in the high canopy, where ant mosaics are present, but weaker in the lower canopy, where turnover should increase more gradually.

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. 1). 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. 1). The ground was relatively level within the plot without steep hillsides or ridges (Dial et al. 2004a). The forest trees of the plot consisted of 11 trees from four families, 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 and Table 1 in Dial et al. 2004a for details of tree species), and stood over an overstory of unidentified trees.

2.2 Field sampling

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 the 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. 1). 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).

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. 1). 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 ground (Fig. 1). 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. In total, we obtained and identified ant assemblage samples for 63 out of 86 sampling points with 14 samples having no ants and 9 samples having been lost between sampling and analysis. 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.

2.2.2 Microclimate and microhabitat 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 is a reflection of 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. 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 Distribution pattern of 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 interval) at which the ants were sampled. 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

In order to understand how ant assemblages changed vertically and horizontally, we first applied linear regression models using the abundance ($\ln(x+1)$ transformed) and richness of ants in each sampling point as response variables, x , with vertical height as continuous explanatory variable and horizontal position of vertical transects as categorical explanatory variable. We then used both abundance-based ($\ln(x+1)$ transformed) assemblage data and species presence/absence data for the following assemblage composition analyses. Two sampling points (comprising one ant individual each) from one emergent layer were excluded from the analyses due to the lack of other replicates at this height level, resulting in total of 61 ant assemblages as our sample size. 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. To keep sample size same for analyses in vertical and horizontal directions, we combined the 12 vertical levels into six vertical groups for NMDS analyses. We tested for statistical significance of these groupings by analyses of between-point assemblage presence/absence variances using the *adonis* function in the *vegan* package (999 permutations) (Oksanen et.al. 2013, R Core Team, 2013). We then calculated the pairwise assemblage dissimilarity across sampling points and further partitioned it into assemblage turnover (balanced variation in abundance) and assemblage nestedness (abundance gradient) between each pair of samples to understand which component drives beta diversity patterns at different horizontal and vertical distances (Si et al. 2017). This will allow us to distinguish the potential effects of resource limitation, which is expected to lead simply to richness gradients but no turnover pattern, as opposed to environmental filtering, which is predicted to lead to species turnover as low canopy species are replaced by high canopy ones. The analyses were calculated 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). For ant assemblage composition analysis, as results from measures using abundance-based pairwise Bray-Curtis dissimilarity and presence-absence based Jaccard species dissimilarity were similar, we only present results using abundance-based pairwise Bray-Curtis dissimilarity in the main text (see online supplementary materials for presence-absence analyses).

We used four different methods to quantify the distance between sampling points: 1) straight line distance between points, 2) maximum surface travel distance, 3) horizontal distance between points, and 4) vertical distance between points. To simplify distance calculations, we assumed that all sampling points were on a straight line from above when calculating the distance between points, although there were some small deviations from this. Straight line distance modelled the case where there was vegetation structure to directly connect the two sampling points for ant movement (Fig. S1). Maximum surface travel distance was calculated as the horizontal distance between the sampling points added to the vertical height of each sampling point above the ground, modelling the scenario where the ground provides the only horizontal connectivity between two points (Fig. S1). We conducted Multiple Regression on Distance Matrices (MRM) using the *MRM* function in the *ecodist* package (Goslee and Urban 2007) to test for relationships between different distance measures and total pairwise dissimilarity, assemblage turnover and nestedness. The tests of significance of MRM coefficients were performed using 1000 permutations.

We then tested the effects of distance on assemblage dissimilarity between and within vertical transects and vertical strata. We first grouped the assemblages within the same vertical transect/vertical stratum, and then tested effects of horizontal/vertical distance on pairwise assemblage dissimilarity between transects/strata

by MRM. To measure within vertical transect/vertical stratum patterns, we conducted post-hoc MRM tests on vertical/horizontal distance effects of pairwise assemblage dissimilarity across sampling points within each transect and stratum. We then conducted linear regression to compare the mean assemblage dissimilarity value and linear effects of distance on pairwise dissimilarity across two dimensions by comparing the intercept and the slope from the MRM analyses of each transect/stratum. To test for the different horizontal turnover patterns between vertical strata expected if ant mosaics effect is present, we conducted linear regression with horizontal pairwise dissimilarity within each stratum as the response variable, horizontal distance and vertical height as well as their interaction as explanatory variables.

Correlates of ant assemblage distribution patterns We conducted constrained ordinations to further 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 *decorana* function in 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 first checked the collinearity among all explanatory variables using *vif.cca* function to reduce redundancy in the model. Among all microclimate and microhabitat factors, no strong collinearity ($VIF < 10$) was been detected and so all predictors were included in the Canonical Correspondence Analysis (CCA). We then conducted CCA ordinations using *ccafun* function in the vegan package with all explanatory variables (air temperature, relative humidity, and PPFD). We conducted backward model selection using *ordistep* function in the vegan package to identify the most significant variables in 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 Distribution pattern of microclimate and microhabitat structure

We found high horizontal and vertical variation in microclimate (air temperature: $R^2 = 0.92, F_{7, 59} = 47.72, P < 0.01$; relative humidity: $R^2 = 0.91, F_{7, 59} = 81.96, P < 0.01$) and microhabitat structure in our study site (Fig. 2). In general, air temperature increased and relative humidity decreased with vertical height based on linear regression model (Fig. 2). In addition, we found significant effects of horizontal position on temperature and humidity (Table S2). The estimated vertical change in air temperature was 0.13°C per 10 m, while estimated horizontal change was 0.36 °C per 10 m (Table S2). The relative humidity was estimated to decrease 1.4% per 10 m vertical increase, and the horizontal variation was also 1.4% per 10 m horizontal distance. The photosynthetic photon flux density (PPFD) increased with vertical height (as PPFD was normalized within each vertical transect, we could not compare this across transects, $R^2 = 0.35, F_{1, 62} = 32.84, P < 0.01$; Table S2, Fig. 2). 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; $R^2 = 0.22, F_{6, 48} = 2.32, P = 0.05$; Table S2, Fig. 2).

Distribution of ant assemblages along vertical and horizontal gradients

In total, 35,710 individual ants from 138 species in 31 genera were sampled. Both ant abundance ($\ln(X+1)$ transformed, $R^2 = 0.67, F_{7, 59} = 2.32, P < 0.01$) and richness ($R^2 = 0.66, F_{7, 59} = 16.65, P < 0.01$) significantly decreased with vertical height, and varied across transects (horizontal positions) (Table S3, Fig. 3). Both NMDS plots and adonis analysis showed clustering of ant assemblages both vertically and horizontally (Fig. S2; adonis analysis (abundance based), vertical stratification: $F = 1.8, R^2 = 0.09, P = 0.01$; across transects: $F = 6.4, R^2 = 0.39, P = 0.001$). Dissimilarity partitioning revealed that the pairwise assemblage dissimilarity between sampling points was largely composed by assemblage turnover, meaning the pairwise dissimilarity was mostly explained by replacement of assemblage composition between sampling points. Using either straight line distance or maximum surface travel distance calculated, we detected a significant increase in total (unpartitioned) pairwise dissimilarity with increasing distance between sampling

points (MRM analyses; Table 1, Fig. 4). While no distance effects were detected in turnover, there were positive effects of distance on the nestedness component of pairwise dissimilarity. Both vertical and horizontal distance showed significant positive effects on total pairwise dissimilarity between sampling points. The effect size of vertical distance on pairwise dissimilarity of ant assemblages was slightly higher than that of horizontal distance, but the explanatory power of both predictors was low (Table S4).

When pooling the data of sampling points within the same transect or vertical stratum to examine distance-decay patterns between transects/strata, we observed strong effects of vertical distance on pairwise dissimilarity indexes between vertical strata. In contrast, we found no effects of horizontal distance on pairwise assemblage dissimilarity between transects (MRM analyses, Table 2, Fig. 5). When comparing across the same distances vertically and horizontally, pairwise dissimilarity was consistently higher horizontally than vertically (Table 2, Fig. 5).

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: $R^2 = 0.60$, $F_{1, 17} = 25.03$, $P < 0.01$, Fig. 6C). However, the effects of vertical distance on pairwise dissimilarity was more apparent and much stronger than that of horizontal distance, presenting a distance-decay pattern within each transect (linear regression: $R^2 = 0.73$, $F_{1, 17} = 46.45$, $P < 0.01$, Fig. 6D). We did not find differing horizontal turnover of ant assemblages in different vertical strata (Fig. 6A, Table 3). We also did not detect significant interactive effects between horizontal distance and vertical height on horizontal pairwise dissimilarity of ant assemblages within each vertical stratum (linear regression: $R^2 = 0.005$, $F_{3, 127} = 0.22$, $P < 0.89$; coefficient of horizontal distance: $p = 0.77$; coefficient of vertical height: $p = 0.95$; horizontal distance * vertical height: $p = 0.73$). Hence, change in horizontal dissimilarity of assemblages did not depend on height, as would be expected if ant mosaics were driving more rapid increase in dissimilarity at greater heights in the canopy.

3.3 Explanatory factors for ant assemblage distribution patterns

Results from Canonical Correspondence Analysis (CCA) and backward model selection suggested both air temperature and relative humidity significantly associated with ant assemblage composition, while PPFD and total leaf area did not show significant effects (Table 4, Figure S5).

4 Discussion

We observed different patterns in species assemblage distribution over 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. The replacement of individuals and species, rather than their loss is the major component of total assemblage dissimilarity both vertically and horizontally, indicating a potential environmental filtering process in maintaining high biodiversity across small spatial scales (Baselga 2010). We found consistently greater horizontal turnover in ant assemblages than that observed at comparable vertical distances. However, increase in turnover with distance was only detected vertically, but not horizontally, with the high species turnover between horizontal positions being independent of distance. The observed patterns are likely associated with continuous directional changes in environment (i.e., microclimate) and resources vertically, and stochastic variation in environment and resource, 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 distribution pattern of microclimate variables in our study plot is in line with other studies: 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 essential 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 not only result 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 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). However, partitioning analyses of vertical pairwise dissimilarity demonstrated that the changes in ant assemblages was mostly driven by the turnover of the assemblage rather than the nestedness of assemblage, which implicated that environmental filtering, rather than resource limitation is a more plausible explanation (i.e. different resources, rather than just less of the same resources). 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 rain forest of Mexico, 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 can 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 lessened in Asian versus American tropics (Dial et al. 2004a). Such barriers between individual trees could make each tree canopy function as an island within the forest (Southwood and Kennedy 1983, Adams et al. 2017).

We did not find any evidence to support the existence of ant mosaics at the scales sampled, since turnover was not higher in the upper canopy, where ant mosaics are more likely to influence community structure (Ribeiro et al. 2013, Yusah et al. 2018). However, previous work conducted close to our study site has found evidence for segregation between species in the high canopy (Yusah et al. 2018). This could be because our horizontal sampling grain was 20 m, and hence most adjacent horizontal samples might already fall in different territories, on different trees, with the exception of species with very large territories such as *Dinomyrmex gigas* (Pfeiffer and Linsenmair 2001). This is supported by the high horizontal turnover in species composition that we observed, regardless of distance across all heights in the canopy.

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. The high turnover of the ant assemblages across short horizontal and vertical distances explains how a high proportion of local biodiversity of arthropods can be detected by comprehensive sampling of the ground and

canopy at small spatial scales (Basset et al. 2012). While previous studies have pointed out the importance of including both canopy and understory communities when examining assemblage composition at large spatial scales (Ashton et al. 2016), our results suggest that comprehensive sampling covering multiple horizontal and vertical planes may allow detection of a large proportion of certain species that utilize multiple dimensions of the space, even when sampling a relative small area of the habitat. Future sampling across multiple vertical and horizontal replicates at microhabitat scales for various taxa, particularly for groups that are sensitive to microclimate and with limited dispersal abilities such as non-flying arthropods, are needed to test the generality of high community dissimilarity over small horizontal distances.

Our study highlights the great conservation value of primary tropical rain forest in supporting high diversity of arboreal arthropods. Compared with disturbed forest, primary tropical rain forest exhibits higher complexity in vegetation structure, greater level of vertical stratification and larger vertical distances due to the presence of taller trees (Klimes et al. 2012, Liu et al. 2016). For instance, in oil palm plantation, which has displaced large areas of forest in tropical Asia (Fitzherbert et al. 2008), canopy ant species richness is 52% lower compared with primary rain forest, possibly due to the simplification of canopy structure (Fayle et al. 2010). The observed high beta diversity supported by vertical forest layers in our study indicates a potential risk of biodiversity loss among arboreal insects with the reduction of these important vertical niches through logging and conversion to plantation. The heterogeneity in microclimates of rain forest may also increase the climate change resilience of tropical species by providing them high microclimate heterogeneity to track their optimal climatic niche for activity (Scheffers et al. 2013, Pincebourde and Suppo 2016).

5 Conclusion

Our study revealed high spatial variation in ant communities in both horizontal and vertical dimensions over small spatial scales. We detected increasing difference in 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 scales. These patterns are associated with variation in air temperature and relative humidity. Connectivity may also play a role in shaping the high turnover of ant assemblages horizontally. Although we found no evidence for patterns congruent with the presence of an ant mosaic, we are unable to rule out potential influences from other biotic factors that are correlated with abiotic gradients. 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.

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

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- Table 1. Effects of total distance on pairwise dissimilarity of ant assemblage between sampling points based on Multiple Regression on Distance Matrices (MRM). Coefficients with statistical significance show in boldface.

Model factor	Response	Coefficient	Adjusted R ²
Maximum surface distance	Assemblage turnover	-7.50e-05	1.02e-04
	Assemblage nestedness	0.001	0.02
	Total dissimilarity	0.001	0.05
Straight line distance	Assemblage turnover	-3.79e-05	1.47e-05
	Assemblage nestedness	0.001	0.03
	Total dissimilarity	0.001	0.07

Table 2. Effects of horizontal and vertical distance on pairwise assemblage dissimilarity between vertical transects and across vertical strata based on Multiple Regression on Distance Matrices (MRM). Coefficients with statistical significance show in boldface.

Model factor	Response	Estimates	Adjusted R ²
Intercept	Assemblage turnover	0.53	0.13
horizontal distance		0.002	
Intercept	Assemblage nestedness	0.29	0.09
horizontal distance		0.002	
Intercept	Total dissimilarity	0.82	0.07
horizontal distance		0.0003	
Intercept	Assemblage turnover	0.32	0.49
vertical distance		0.005	
Intercept	Assemblage nestedness	0.10	0.04
vertical distance		0.001	
Intercept	Total dissimilarity	0.42	0.019
vertical distance		0.007	

Table 3. Effects of vertical and horizontal distance on pairwise dissimilarity of ant assemblages within each transect and vertical stratum based on results from Multiple Regression on Distance Matrices (MRM) analysis. Coefficient value with statistical significance show in boldface.

Transect	Intercept	Coefficient
T1	0.519	0.010
T2	0.502	0.010
T3	0.764	0.003
T4	0.586	0.008
T5	0.356	0.013
T6	0.608	0.005
T7	0.273	0.005
Vertical stratum	Intercept	Coefficient
H1	0.89	4.236e-4
H2	0.768	0.002
H3	0.950	-6.573e-4
H4	0.907	-8.112e-4
H5	0.882	-2.490e-4
H6	0.955	-0.001
H7	0.488	0.004
H8	0.883	6.590e-4
H9	0.913	-5.485e-5
H10	0.994	-0.001
H11	0.883	0.001
H12	0.837	0.001

Table 4. Backward model selection result for canonical-correlation analysis (CCA). Significant *P* values are labeled with *.

Full model (ant assemblage composition ~ Total leaf area + PPFD + air temperature + relative humidity)

Explanatory factors	Df	AIC	F	P value
Total leaf area	1	225.51	0.948	0.530
PPFD	1	225.49	0.929	0.505
Relative humidity	1	226.36	1.735	0.010*
Air temperature	1	227.33	2.652	0.005*

Model without “Total leaf area” (ant assemblage composition ~ PPFD + air temperature + relative humidity)

Explanatory factors	Df	AIC	F	P value
PPFD	1	224.49	0.911	0.505
Relative humidity	1	225.37	1.741	0.010*
Air temperature	1	226.30	2.641	0.005*

Model without “Total leaf area” and “PPFD” (ant assemblage composition ~ air temperature + relative humidity)

Explanatory factors	Df	AIC	F	P value
Relative humidity	1	225.25	2.660	0.005*
Air temperature	1	225.35	2.759	0.005*

Figure 1. Study site and design: A) habitat photo of the sampling plot; B) Map of Sabah with elevation gradient presented; 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).

Figure 2. Heatmaps along with scatter plot showing the horizontal and vertical distribution at 5 m vertical interval of (A) air temperature, (B) relative humidity, (C) photosynthetic photon flux density (PPFD), and (D) total leaf area. Color with higher saturation indicate higher value of the environmental variables.

Figure 3. Heatmaps along with scatter plot showing vertical and horizontal distribution of (A) species abundance ($\ln(x+1)$ transformed) and (B) species richness. Color with higher saturation indicate higher value.

Figure 4. Linear relationships between pairwise distance and abundance based pairwise dissimilarity of ant assemblage when using A) maximum surface travel distance and B) straight line distance between sampling points. The pairwise dissimilarity (green points) is partitioned by nestedness (yellow points) and turnover (blue points). Grey bands show 95% confidence interval. Solid line indicates significant relationship. Dissimilarity close to one indicates that two assemblages are dissimilar, while dissimilarity close to zero indicates that they are similar.

Figure 5. Effects of horizontal (circle points) and vertical distance (triangle points) on abundance based pairwise dissimilarity of ant assemblage between transects and vertical strata. Pairwise dissimilarity (green points) is partitioned by nestedness (yellow points) and turnover (blue points). Grey bands show 95% confidence interval. Solid line indicates significant relationship. Dissimilarity close to one indicates that two assemblages are dissimilar, while dissimilarity close to zero indicates that they are similar.

Figure 6. A) Relationship between vertical distance and pairwise dissimilarity of ant assemblages within each transect. Different colors of dot point and trend line indicate different transect. B) Relationship between horizontal distance and pairwise dissimilarity of ant assemblages within each vertical strata. Darker points and trend line indicate higher vertical stratum. C) 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 transect/stratum. Model intercept

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 incorporate data that are 1.5 * IQR. Data beyond this are plotted individually.







