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LONG-TERM IMPACTS OF FOREST FRAGMENTATION AND LAND USE CHANGE ON ANT COMMUNITY IN TROPICAL FOREST IN SABAH, MALAYSIA

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ABSTRACT

Tropical rainforests are among the most biodiverse ecosystems on earth, yet they are increasingly threatened by human activities such as deforestation, logging, and agricultural expansion. A major consequence of these disturbances is forest fragmentation, which disrupts habitat structure, reduces landscape connectivity, and alters species assemblages. Ants as ecological importance and sensitivity to environmental changes, are effective bioindicators for assessing biodiversity responses to such disturbances. This study investigates the long-term impacts of forest fragmentation and land-use change on ant communities in the Bornean tropical rainforest. Ant assemblages were sampled across three time points, pre fragmentation (2011), four years after (2015), and eight years after (2019) in forest fragments of varying sizes (1-ha, 10-ha, and 100-ha), matrix habitats, logged forest, oil palm plantations, and old-growth forest, representing a gradient of land-use intensity. Canopy ants were collected using insecticidal fogging, while leaf-litter ants were sampled via Winkler extraction. In total, 106,084 individual ants from 72 genera were recorded across all sampling years. Results revealed a significant decline in canopy ant abundance over time, particularly by 2019, indicating strong negative impacts of fragmentation on arboreal ant communities. In contrast, leaf-litter ant abundance increased in disturbed habitats suggesting a degree of resilience or adaptability among ground-dwelling taxa. Notably, the genus *Plagiolepi*s was more prevalent in fragmented forests, whereas oil palm plantations harbored the most depauperate ant assemblages. These findings demonstrate contrasting responses between canopy and leaf-litter ants to habitat disturbance over time, importance of incorporating both vertical strata and long-term monitoring into biodiversity assessments.

Keywords: Arboreal ant; leaf litter ant; forest fragment; Formicidae; land use changes

ABSTRAK

Hutan hujan tropika merupakan antara ekosistem paling melimpah di dunia, namun kini semakin terancam akibat aktiviti manusia seperti penebangan hutan, pembalakan, dan pertanian. Salah satu akibat utama gangguan ini ialah fragmentasi hutan, yang mengganggu struktur habitat, mengurangkan keterhubungan landskap, serta mengubah susunan komuniti spesies. Oleh kerana kepentingan ekologi dan kepekaan semula jadi terhadap perubahan persekitaran, semut dijadikan bioindikator yang berkesan untuk menilai tindakbalas biodiversiti terhadap gangguan tersebut. Kajian ini mengkaji kesan jangka panjang fragmentasi hutan dan perubahan guna tanah terhadap komuniti semut di hutan hujan tropika Borneo. Komuniti semut disampel pada tiga titik masa iaitu sebelum fragmentasi (2011), empat tahun selepas (2015), dan lapan tahun selepas fragmentasi (2019) pada pelbagai saiz fragmentasi hutan (1 ha, 10 ha dan 100 ha), habitat matriks, hutan telah tebang, ladang kelapa sawit serta hutan tua, yang mewakili kecerunan intensiti guna tanah. Semut kanopi dikumpulkan menggunakan kaedah penyemburan asap beracun, manakala semut sarap daun dikumpulkan mengggunakan kaedah Winkler. Secara keseluruhan, sebanyak 106,084 individu semut daripada 72 genera direkodkan sepanjang tiga tahun persampelan tersebut. Dapatan menunjukkan penurunan ketara dalam kelimpahan semut kanopi dari masa ke masa, terutamanya pada tahun 2019, menandakan kesan negatif yang kuat akibat fragmentasi hutan terutamanya komuniti semut arboreal. Sebaliknya, kelimpahan semut sarap daun meningkat dalam habitat terganggu, ini mungkin dari daya tahan atau keupayaan penyesuaian yang ada pada spesies semut sarap daun sendiri. Hasil dari kajian ini, genus Plagiolepis banyak ditemui dalam hutan fragmentasi, manakala jenis guna tanah seperti ladang kelapa sawit menampung komuniti semut yang paling kurang. Dari kajian ini juga, menunjukkan tindakbalas yang berbeza antara semut kanopi dan semut sarap daun terhadap gangguan habitat dari masa ke masa, sekali gus menekankan pentingnya memasukkan kedua-dua strata menegak dan pemantauan jangka panjang dalam penilaian biodiversiti.

Kata kunci: Semut arboreal; semut sarap daun; fragmentasi hutan; Formicidae; perubahan guna tanah

INTRODUCTION

Tropical rainforests are globally recognized as biodiversity hotspots, supporting a vast number of endemic species (Sodhi et al. 2010). Invertebrate diversity is particularly high in these ecosystems, with estimates suggesting that a single hectare may harbor around six million invertebrate individuals and approximately 18,000 species (Basset et al. 2012; Ewers et al. 2015). This underscores the ecological richness and complexity of tropical forests. However, these ecosystems are increasingly threatened by deforestation and land-use changes. By 2012, an estimated 150 million hectares of forest had been cleared, largely for agricultural expansion (Edwards et al. 2019). In Asia alone, around 79% (25 million hectares) of forest conversion was driven by agriculture (FAO 2022). Such transformations including agriculture, logging, and plantation development are major contributors to habitat loss and forest fragmentation (Malhi et al. 2014). These activities significantly impact biodiversity, as shown by studies linking plantation development to reduced tropical forest species richness (Newbold et al. 2014).

Forest fragmentation further contributes to ecological degradation by breaking continuous habitats into smaller, isolated patches (Hansen et al. 2020). These results change variation in habitat quality, often characterized by increased human disturbance, resource exploitation, and invasions by non-native species (Cardozo et al. 2021). These changes reduce ecosystem functionality, leading to declines in species richness and the loss of vital ecosystem services (Rubiana et al. 2015). Fragmented landscapes often consist of small habitat patches that function like ecological islands. Such isolation, fragmentation also limits species movement, increases extinction risk (Luther et al. 2020), and alters patterns of abundance, richness, and community composition (Arroyo-Rodríguez et al. 2020). Species found in these fragments typically represent a subset of those in intact forests (Câmara et al. 2017). The loss of forest area, coupled with increased edge effects and shrub encroachment, further exacerbates habitat degradation (Arroyo-Rodríguez et al. 2020; Fahrig 2003).

In Sabah, approximately 1.54 million hectares of land have been converted to oil palm plantations since 2019 (MPOB 2019). This large-scale land-use conversion has resulted in extensive forest fragmentation, caused by the separation between remaining forest patches and surrounding plantation areas. Such transformation poses serious ecological concerns, contributing not only to local biodiversity loss but also to global issues such as greenhouse gas emissions, soil degradation, and the disruption of essential ecosystem functions (Alroy et al. 2017; Barlow et al. 2007; Silalertruksa et al. 2017). The conversion of natural forests into monoculture plantations often favors generalist and competitively dominant species, leading to species homogenization and the decline of specialists and sensitive taxa (Alroy 2017; Foster et al. 2011; Socolar et al. 2016). This biotic simplification may further disrupt ecosystem processes, as dominant species often fail to perform the same ecological functions as those lost (Etard et al. 2022; Rebeiro et al. 2022).

Ants are particularly valuable bioindicators of such ecological changes due to their sensitivity to disturbance, ecological diversity, and critical functional roles. Previous studies in tropical ecosystems have shown that fragmentation and land-use change reduce ant diversity, alter community composition, and promote disturbance-tolerant species (Câmara et al. 2017; Hernández-Flores et al. 2020; Rebeiro-Neto et al. 2016). However, in Sabah, little is known about the long-term effects of forest fragmentation and land-use change on ant communities, particularly across different forest strata such as the canopy and leaf litter layers.

Therefore, investigating ant communities in landscapes experiencing forest fragmentation and land-use change is essential to assess the ecological consequences of such disturbances. Variations in ant species richness, abundance, and community composition can provide valuable insights into the extent of habitat alteration and its implications for ecological functioning. Furthermore, the ease with which ants can be sampled and resurveyed over time (Alonso & Agosti 2000) makes them an ideal model group for evaluating long-term biodiversity responses in tropical ecosystems such as those in Sabah.

This study addresses this gap by examining the long-term impacts of forest fragmentation and land-use change on ant communities in a Sabah. Using data collected across three time periods, pre-fragmentation (2011), four years post-fragmentation (2015), and eight years post-fragmentation (2019). The study evaluates temporal changes in canopy and leaf-litter ant abundance, species richness, and community composition. By identifying patterns of resilience and vulnerability among species, this research aims to improve understanding of biodiversity responses to anthropogenic landscape change and support evidence-based conservation strategies for maintaining the ecological roles of functionally important insect communities.

MATERIALS AND METHODS

Study Area

This study was conducted in Sabah, Borneo. We focused on four distinct habitat types, including an experimental forest fragmentation area located in the Kalabakan Forest Reserve Class 5, managed by Yayasan Sabah, as well as three control habitats. The control sites comprised an old-growth forest (OG) within the Maliau Basin Conservation Area in the Tongod District, an oil palm plantation (OP) managed by Benta Wawasan, and a twice-logged forest (LF) situated in the Kalabakan District. All study sites are part of the broader Stability of Altered Forest Ecosystems (SAFE) Project (Ewers et al. 2011) (Figure 1).

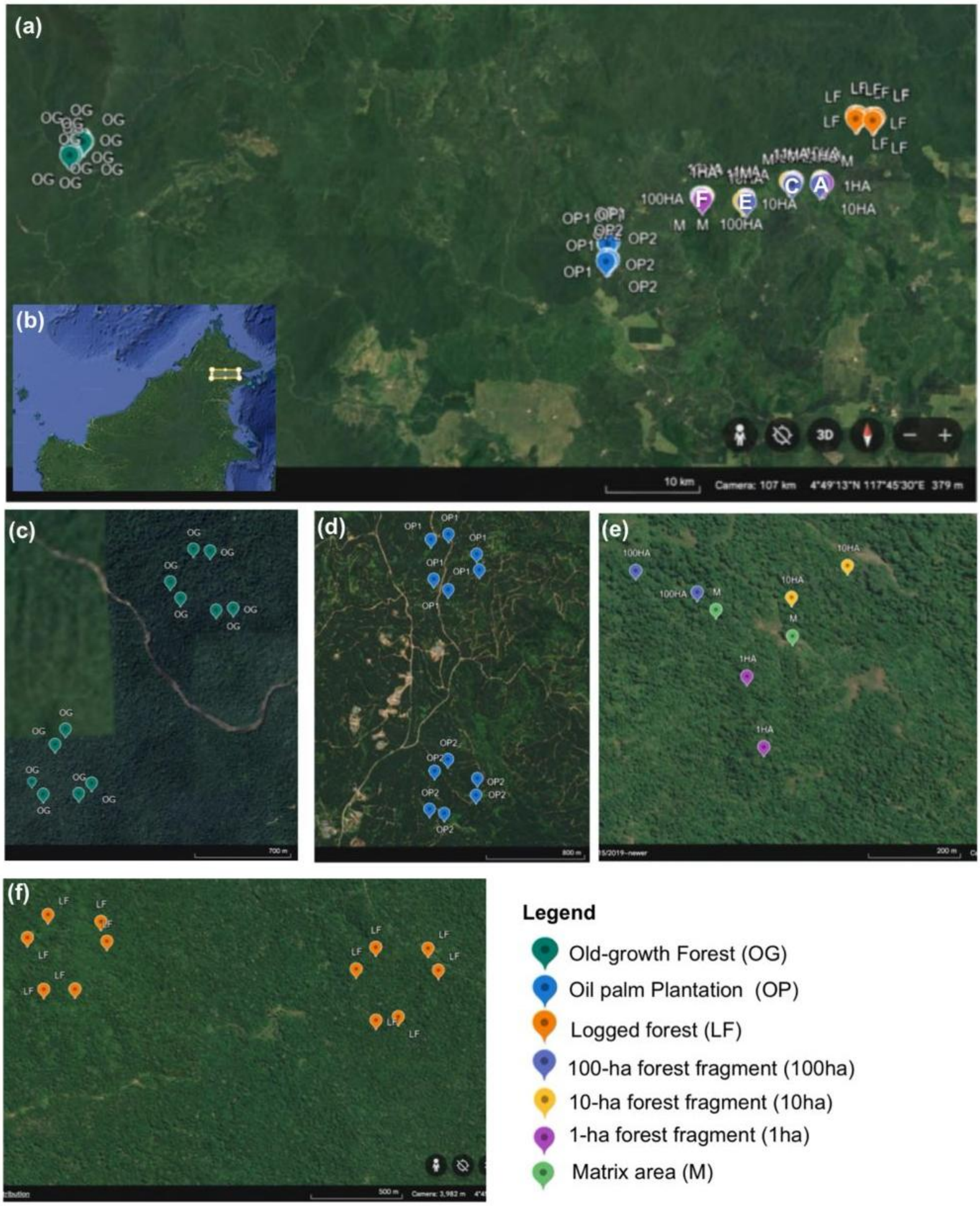


Figure 1. Map of site sampling in SAFE Project. (a) The positions of OG, OP, fragment area (blocks A, C, E, F) and LF in map. (b) The location of SAFE Project in Borneo's map. The position and pattern of site sampling for (c) Oil-growth Forest, (d) Oil palm plantation, (e) One plot for fragment area, and (f) Log Forest area

Sampling Design

Our study design was built upon the well-established SAFE Project framework, a robust system incorporating forest fragments of 100-ha, 10-ha, and 1-ha, along with the surrounding matrix areas. For this research, sampling was conducted exclusively within four specific forest fragmentation blocks (A, C, E, and F), chosen because they were the only blocks available for both the 2011 and 2015 sampling periods. Samples were collected from two of the "second order" points of forest patch size for each block, resulting in a total of 32 sampling sites dedicated to the fragmentation experiment.

In addition to the fragmentation sites, control sites were incorporated to provide vital comparative baselines for ant species diversity. These included old-growth forest (OG), oil palm plantation (OP), and continuous twice-logged forest (LF). For each control habitat, 12 distinct sampling sites were established, contributing 36 control sites to the study. This brought the grand total of sampling locations to 68 sites.

Ant Sampling

Ant communities were sampled during three periods (2011, 2015, and 2019) to examine long-term changes in species composition and abundance. A standardized sampling protocol was applied in each year to ensure data comparability. Sampling was conducted daily from April to November under weather permitting, except in 2011, when fieldwork lasted only three months due to logistical constraints.

Fieldwork was conducted only under suitable weather and safety conditions to minimize disruptions caused by rainfall, hunters, or the presence of wild elephants within the study area. All field personnel observed rest days during weekends (for data collection conducted in 2011 and 2019) to ensure consistency in sampling efforts and to maintain safety standards. Ant specimens were collected using two complementary sampling methods designed to target distinct strata of the ant community, thereby providing a comprehensive representation of both leaf litter and canopy assemblages.

Leaf-litter Ant Sampling

Leaf-litter ants were sampled using the Winkler extraction method. In each sampling site, a 1m × 1m plot was established near the center of the area. All leaf litter within the plot was collected and processed using a coarse sieve for four minutes per sample, allowing ants and smaller pieces of litter to fall into a collection sack. The contents of this sack were then left in Winkler litter extractors for three days in a warm dry location out of direct sunlight. To prevent contamination from insecticidal fogging, Winkler sampling was consistently performed one day prior to fogging activities.

Canopy Ant Sampling

Canopy ants were collected using the insecticidal fogging method. A solution of 2.27% Alphacypermethrin, diluted in diesel oil, was dispersed into the tree canopy using a thermal fogger. Fogging was conducted before 6:00 am for four minutes to minimize wind disturbance and enhance canopy penetration (Floren et al. 2014). Beneath each tree, four circular, funnel-shaped 1m^2 collecting trays with attached tubes containing 70% ethanol were positioned to capture ants dislodged from foliage, branches, and trunks. This setup effectively sampled the canopy ant assemblage, although inherent limitations such as uneven fog distribution and partial insect recovery are acknowledged (Adis et al. 1998; Ozanne 2005). The ethanol solution served both as a collection medium and a preservative for the specimens.

Ant Identification

All ants collected were identified to morphospecies level, as comprehensive species-level identification was constrained by the availability of taxonomic experts. Identification was performed to genus level, with individual morphospecies assigned unique numerical codes. To maintain consistency across sampling years, morphospecies from 2011 and 2015 were re-examined and cross-referenced with the 2019 dataset. Identification followed the keys provided by Hashimoto (2003). For each morphospecies, the number of individuals and its morphospecies code were recorded for analysis.

Statistical Analyses

Ant communities were analyzed separately for canopy and leaf litter habitats due to differences in sampling methods and effort. To assess differences in ant species abundance and morphospecies richness across sampling years and land-use types, we employed the Kruskal–Wallis test, a non-parametric alternative to two-way ANOVA that is appropriate for comparing groups with non-normally distributed data. Data normality was assessed using the Shapiro–Wilk test (Mishra et al. 2019). A significance level of $P<0.05$ was used to determine statistical significance.

When significant effects were detected using the Kruskal–Wallis test, pairwise post hoc comparisons were conducted using the Wilcoxon rank-sum test. To control for false positives resulting from multiple comparisons, we applied the Bonferroni correction (Narkevich et al. 2020). The Wilcoxon test was chosen for its relatively high statistical power compared to more conservative methods such as the Bonferroni–Dunn test (Midway et al. 2020). All analyses were performed in RStudio 4.2.0 using the packages ‘tidyverse’, ‘ggpubr’, and ‘rstatix’ for data handling, visualization, and statistical testing.

Ant community composition across habitat types and sampling years was examined using non-metric multidimensional scaling (NMDS), based on the Jaccard dissimilarity index and presence–absence data. The ordination was performed using the ‘metaMDS()’ function from the vegan package in R (Oksanen et al. 2013), with two dimensions ‘(k = 2)’ and ‘trymax = 100’ iterations to ensure a stable solution. The stress value from the NMDS analysis was used to assess the reliability of the ordination. In this study, the final NMDS solution yielded a stress value of 0.12, indicating a fair fit to the original dissimilarity data. Generally, stress values below 0.05 are considered excellent, values between 0.05 and 0.1 indicate good ordination, values between 0.1 and 0.2 are considered fair and acceptable for interpretation, and values above 0.2 suggest a poor fit (Dexter et al. 2018). To further interpret patterns of community composition, species vectors were included by extracting species scores from the NMDS results. These scores represent the centroid positions of species in the ordination space, reflecting their distributional tendencies across samples. Species located near the edges of the NMDS plot are typically more habitat-restricted, while those closer to the center tend to be generalist species occurring across multiple habitat types. These species vectors provided additional ecological context to the observed clustering patterns among sites.

RESULTS

A comprehensive total of 106,084 individual ants, representing 569 morphospecies, were sampled using both canopy fogging and Winkler extraction methods. In 2011, prior to land-use changes, the highest overall ant abundance was recorded, with 57,741 individuals and 301 morphospecies. Of these, 55,113 were canopy ants (240 morphospecies from 44 genera), and 2,628 were leaf-litter ants (114 morphospecies from 43 genera). By 2015, the total ant abundance decreased substantially to 24,049 individuals, with a similar morphospecies richness of 300. This included 21,633 canopy ants (233 morphospecies, 47 genera) and 2,416 leaf-litter ants (139 morphospecies, 49 genera). In 2019, ant abundance remained relatively stable compared to 2015, with 24,294 individuals, but morphospecies richness increased to 369 across 61 genera. Notably, canopy ant abundance continued to decline, reaching 17,309 individuals (226 morphospecies, 40 genera). Conversely, leaf-litter ants showed a marked increase, reaching 6,985 individuals (233 morphospecies, 51 genera). Overall, canopy ant abundance was highest in 2011 and declined substantially by 2019, while leaf-litter ant abundance was highest in 2019, indicating a potential shift in community structure following fragmentation.

Among individual species ants in the canopy, *Plagiolepis* was the dominant genus across all three study years with 69.42% in 2011, 42.37% in 2015, and 31.83% in 2019. This was followed by *Crematogaster* (2011, 18.81%, 2015, 30.42%, 2019, 26.62%) and *Dolichoderus* (2011: 2.02%, 2015: 3.88%, 2019: 11.75%) as the top three most abundant genera. For canopy morphospecies richness, *Polyrachis* was the most speciose genus, accounting for 16.06% in 2011, 18.61% in 2015, and 27.07% in 2019. In the leaf litter, *Strumigenys* was dominant on abundance in 2011 (22.53%), *Plagiolepis* in 2015 (19.83%), and *Carebara* in 2019 (34.69%). Regarding leaf-litter morphospecies richness, *Strumigenys* was speciose in 2011 (13.38%), followed by *Tetramorium* (8.17%), and *Pheidole* (14.17%).

An Abundance of Ant Canopy and Leaf Litter Group by Habitat

When comparing across years within each habitat (Figure 2a), temporal differences in abundance were observed although most were not statistically significant based on Kruskal–Wallis tests. A marginally significant difference was detected in the Matrix habitat (Kruskal-Wallis test, χ^2 (24) = 8.05, *P=0.0179*), with higher abundance recorded in 2011 and decline abundance in over time. Other habitats such as 100-ha, 10-ha, 1-ha, OG, LF, and OP showed no significant changes in ant abundance over time (*P>0.05).*

Analysis across years within habitats on ant abundance in leaf litter (Figure 2b) showed that overall temporal differences in abundance were limited. Most habitats, including 100-ha, 10-ha, 1-ha, LF, and Matrix, did not show significant changes in ant abundance over time (Kruskal-Wallis, *P>0.05*). However, old-growth forests (OG) and oil palm plantations (OP) displayed significant temporal variation, with both showing increased ant abundance in 2019 compared to earlier years (Kruskal-Wallis test, χ^2 (36) = 14.0, *P=0.000914* and χ^2 (36) = 12.4, *P=0.00198*, respectively). These increases could indicate colonization dynamics or shifts in litter structure and microhabitats that favor certain species in later years.

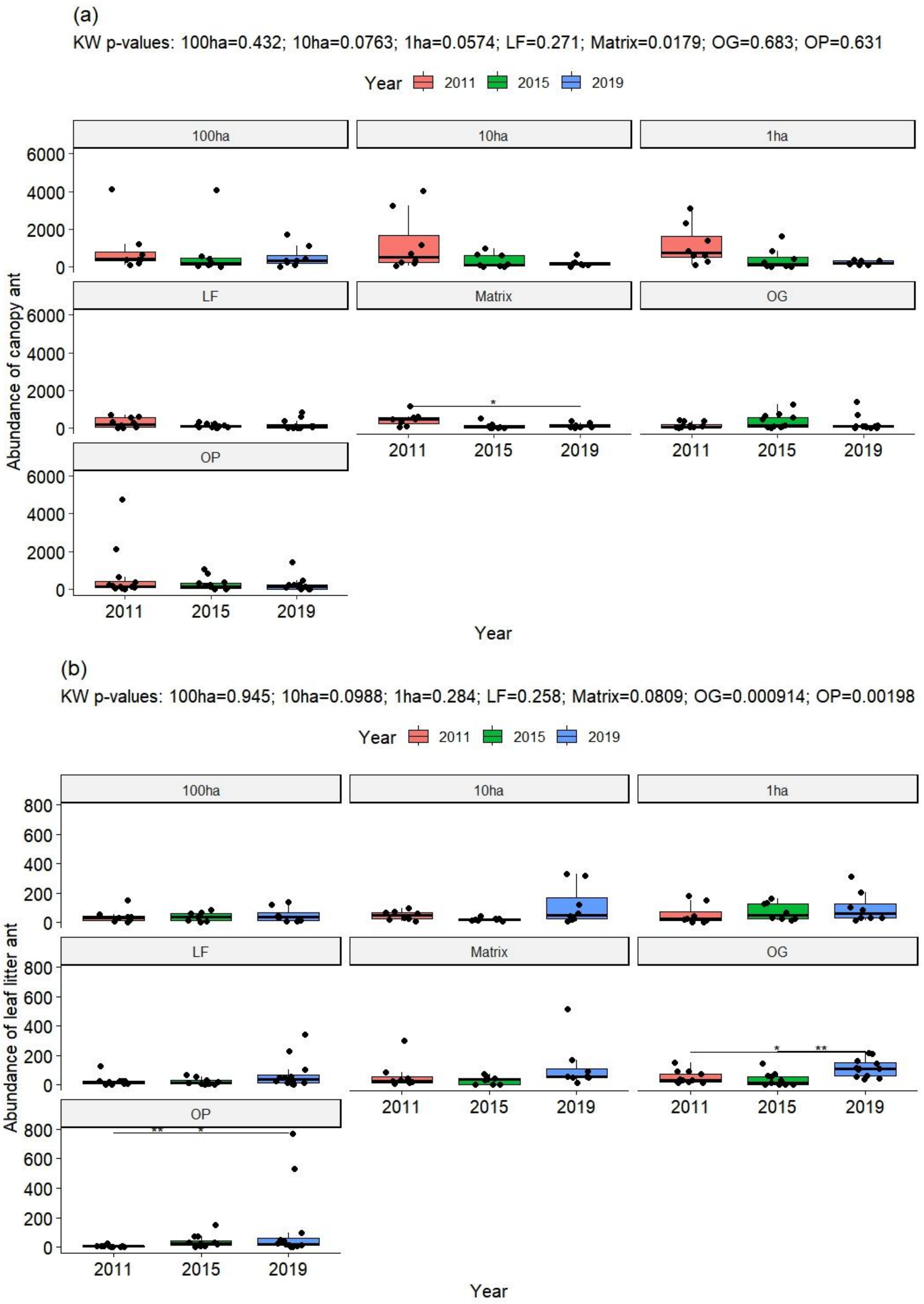
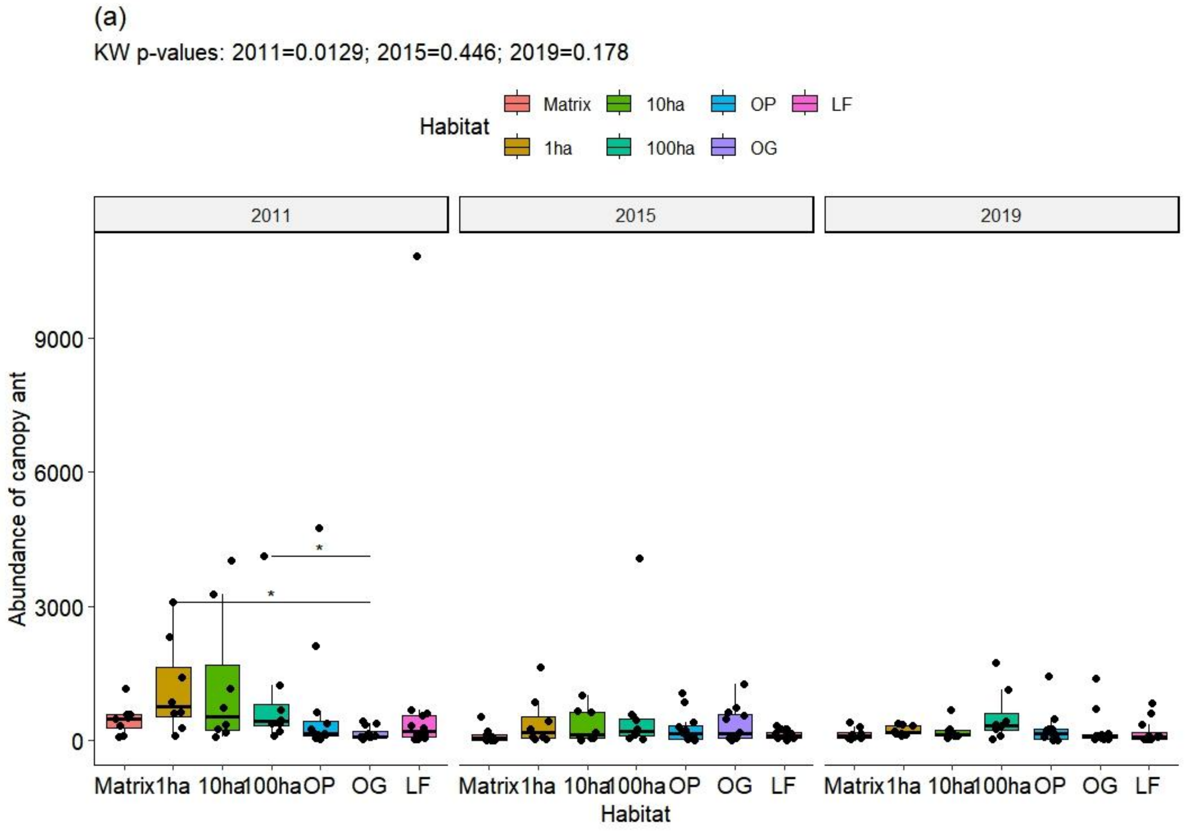


Figure 2. Boxplots showing the abundance of canopy ants across three sampling years (2011, 2015, 2019) within each habitat type in (a) canopy and (b) leaf litter. Kruskal–Wallis (KW) p-values are shown for each habitat to assess temporal differences. Significant pairwise differences are indicated with asterisks (*), one asterisk means significant lower (*) and double asterisk (**) means strongly significant

An Abundance of Ant Canopy and Leaf Litter Group by Year

Our analysis revealed significant temporal variations in abundance of canopy ant among habitat in all three years had a significant effect of habitat on both canopy (Kruskal-Wallis test, χ^2 (6) = 16.20, *P*=0.013, figure 3a) and leaf litter (χ^2 (6) = 24.60, *P<0.001*, figure 3b) ant abundance in 2011. In canopy ant abundance was markedly higher in 1-ha and 10-ha fragments, with significantly lower values in 1-ha and 100-ha with OG. Pairwise comparisons confirmed that 1-ha and 100-ha fragments supported significantly more ants than degraded or anthropogenically altered habitats like matrix and oil palm plantation, also in old-growth area. Meanwhile in leaf litter, old-growth forest (OG) supported significantly greater ant abundance than oil palm and logged forest habitats. Similarly, small fragments (matrix, 10-ha and 100-ha) had higher abundance than OP.

In 2015 and 2019, although overall canopy abundance declined and appeared more evenly distributed across habitats, statistically show no significant differences persisted in the both years canopy (Kruskal-Wallis test, 2015: χ^2 (6) = 5.80, *P*=0.446), 2019: (χ^2 (6) = 8.92, *P*= 0.178) and leaf litter (2015: χ^2 (6) = 8.04, *P=0.235*), 2019: (χ^2 (6) = 10.00, *P=0.123*). Ant abundance appears more even across habitats canopy and leaf litter, with no extreme outliers or dominant groups. This may also be due to stabilization or adaptation of ant communities and long-term homogenization of ant communities due to prolonged fragmentation and land-use changes (Figure 3).



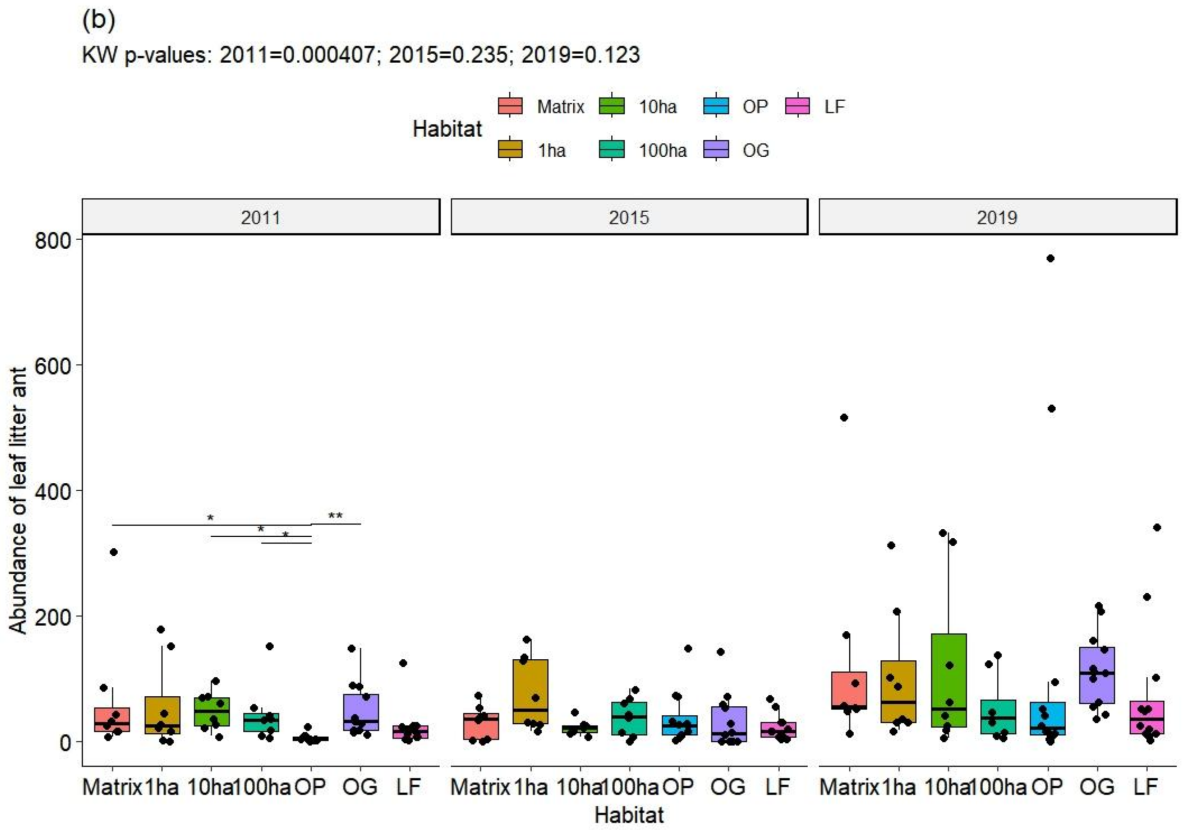


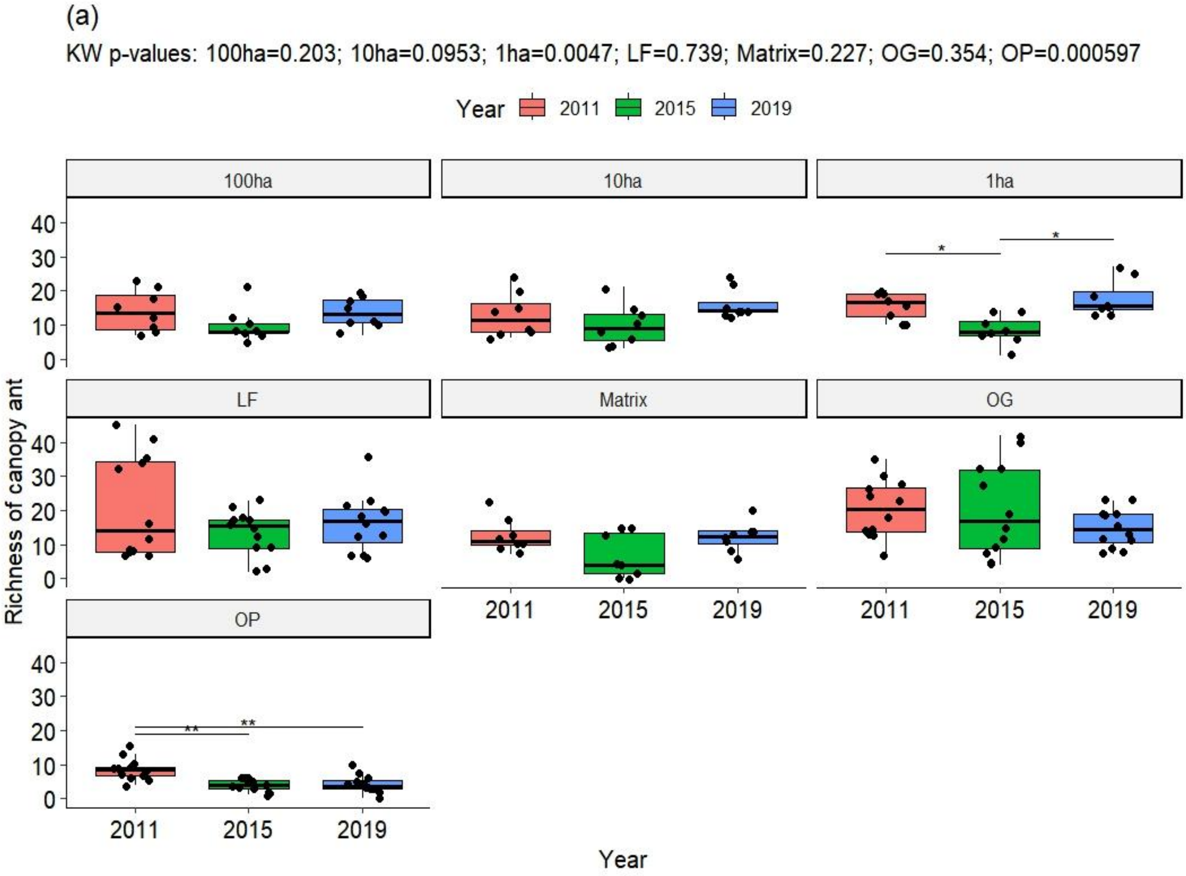
Figure 3. Boxplots showing ant abundance across years in canopy (a) and in leaf litter (b). Only year 2011 had significant meanwhile 2015 and 2019 had no significant difference between difference habitat land use

Analysis of ant abundance across different land-use types and habitats revealed that *Plagiolepis* was the most dominant genus in the canopy, while *Carebara* was consistently dominant in the leaf litter. In the canopy, *Plagiolepis* exhibited the highest number of individuals in the 100-ha, 10-ha, logged forest (LF), and oil palm (OP) habitats, with 12,284 individuals (69.60%), 10,993 individuals (76.78%), 11,287 individuals (64.3%), and 10,264 individuals (67.42%), respectively. In contrast, *Crematogaster* was the most abundant genus in the matrix (M) habitat with 3,268 individuals (55.13%), while *Dolichoderus* was dominant in the old-growth forest (OG) canopy, comprising 1,935 individuals (21.73%) In the leaf litter, *Carebara* was the most abundant genus across all habitats, except in the 1-ha site, where *Lophomyrmex* had the highest number of individuals (n = 315; 16.90%), followed closely by *Carebara* (n = 305; 16.40%). The abundance of *Carebara* in other habitats was as follows, 162 individuals (15.19%) in 100-ha, 342 (23.01%) in 10-ha, 358 (24.72%) in LF, 508 (23.74%) in M, 859 (41.37%) in OP, and 416 (17.87%) in OG.

A Richness of Ant Canopy and Leaf Litter Group by Habitat

The canopy ant richness across different habitats over three time points, notably, statistically significant temporal differences in richness were observed in the 1-ha and OP habitats (Kruskal–Wallis test: χ^2 (24) = 4.70, *P=0.0047* and χ^2 (36) = 14.80, *P=0.000597*, respectively). The 1-ha fragments showed significantly higher richness in 2011 compared to 2015 and 2019, suggesting possible loss of sensitive canopy species over time in small fragments. In contrast, OP habitats consistently had lowest richness across all years, with a significant decline from 2011 to 2015 and 2019. This suggests ongoing degradation or low recolonization potential in highly disturbed monoculture landscapes especially in oil palm plantation who practice the cultivation of the same species. The lack of significant differences in richness over time in larger fragments (100-ha, 10-ha), LF, Matrix, and OG suggests temporal stability in these more structurally intact habitats, possibly due to retained microclimate and canopy connectivity.

For richness ant in leaf litter, significant temporal differences in species richness were observed particularly in OG and OP. In OG, richness in 2019 was significantly higher than in 2015 (Kruskal–Wallis test: χ^2 (36) = 13.20, *P=0.0013*), suggesting a potential recovery or delayed colonization effect post-disturbance. Similarly, OP habitats exhibited a marked increase in richness in 2019 (χ^2 (36) = 6.70, *P=0.0352*), which may reflect secondary succession, adaptation of generalist species, or edge effects facilitating colonization. In contrast, other habitats such as 100-ha, 10-ha, 1-ha fragments, LF, and Matrix did not show statistically significant differences across years (Kruskal-Wallis, all *P>0.05*), although a subtle increase in median richness in 2019 was noted in 10-ha and LF plots (Figure 4). This may suggest relative stability or a slower rate of compositional change in these habitats.



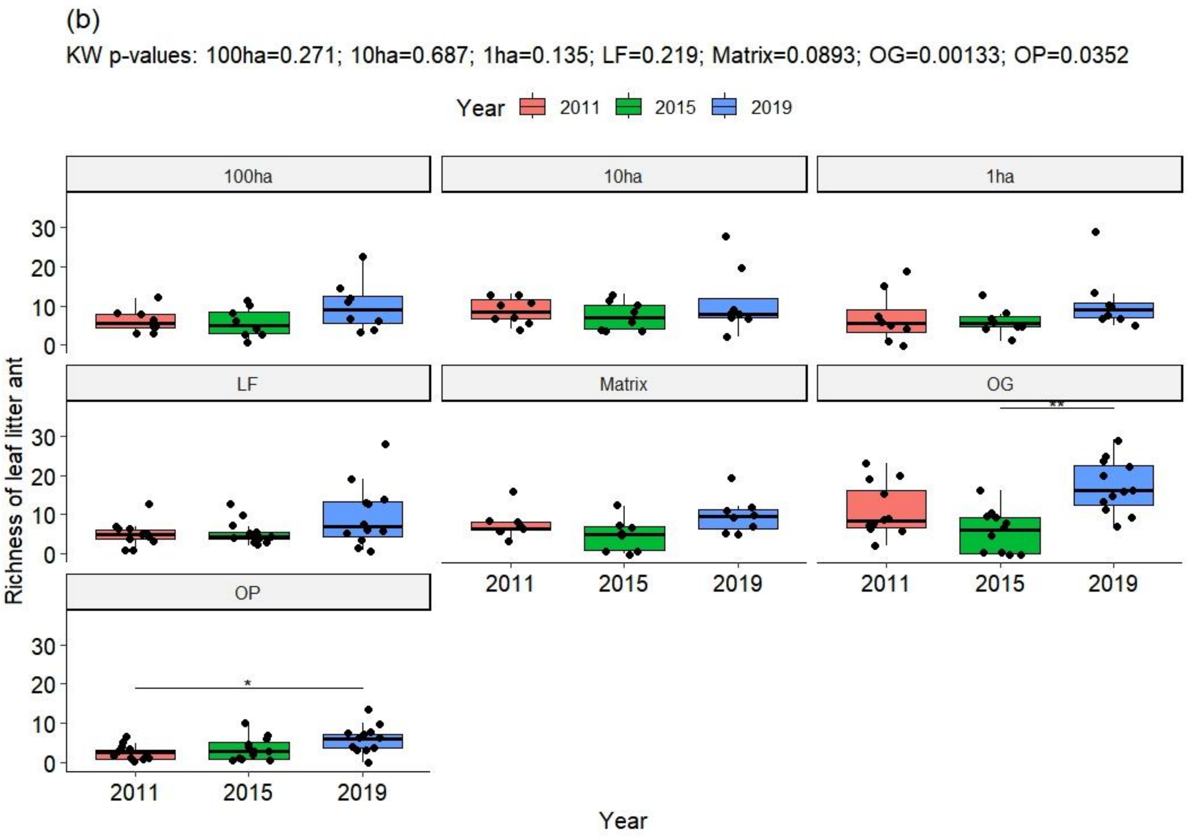


Figure 4. Boxplots showing the richness of canopy (a) and leaf litter (b) ants across three sampling years (2011, 2015, 2019) within each habitat type. Kruskal–Wallis (KW) p-values are shown for each habitat to assess temporal differences. Significant pairwise differences are indicated with asterisks (*)

A Richness of Ant Canopy and Leaf Litter Group by Year

The Kruskal-Wallis test shows significant differences in richness among habitats in all three years: 2011 (χ^2 (6) = 16.50, *P=0.011*), 2015 (χ^2 (6) = 23.90, *P<0.001*), and 2019 (χ^2 (6) = 30.50, *P<0.001*).), indicating that canopy ant richness is strongly influenced by both habitat type and time. In 2011, significantly higher species richness was observed in OG and LF compared to degraded habitats such as the matrix and OP. This pattern suggests that structurally complex and relatively undisturbed forests provide more suitable conditions for diverse canopy ant communities. By 2015, the richness differences became more pronounced. Forested habitats, particularly OG and LF, continued to support significantly higher richness than OP and smaller fragments like 1-ha and matrix. This suggests that while some forest fragments retain moderate diversity, extensive and older forests remain critical strongholds for canopy ant biodiversity. In 2019, the richness disparity widened further. A high number of significant pairwise comparisons show that almost all natural forest habitats (e.g. OG, LF, and fragment areas) supported higher ant richness compared to heavily modified habitats (e.g. OP and matrix) (Figure 5). The lowest richness values were consistently recorded in OP plantations, highlighting the long-term negative effect of intensive land-use change on canopy ant diversity.

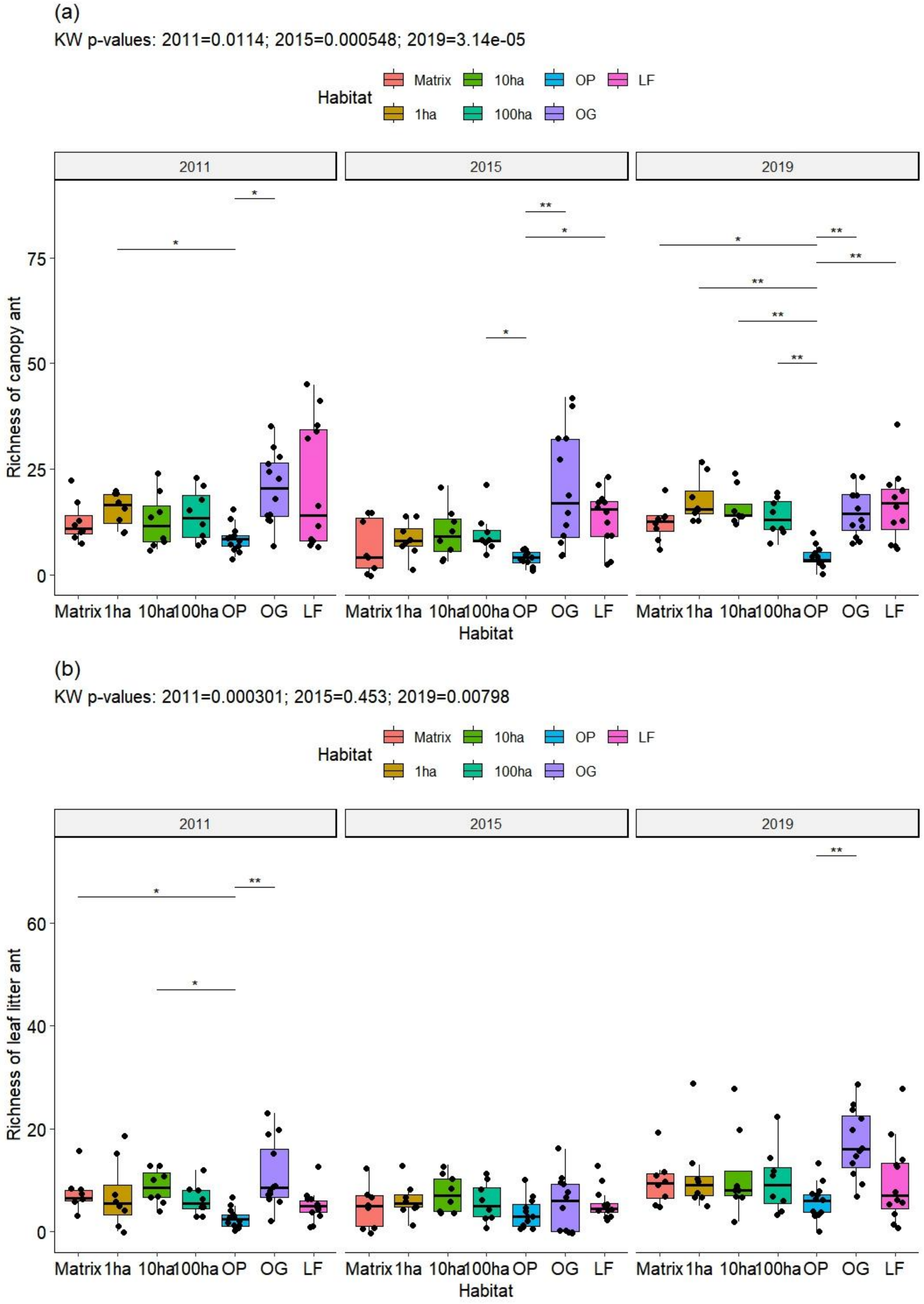


Figure 5. The boxplot show illustrates of morpho-richness across ant in different habitats and years. Richness ant in canopy (a) and richness ant in leaf litter (b), revealing significant variation linked to land-use types and temporal changes

The genus *Polyrhachis* exhibited the highest overall morphospecies richness, particularly within the canopy habitat, where 72 morphospecies were recorded, accounting for 16.44% of the total. This was followed by *Camponotu*s with 60 morphospecies (13.70%) and *Crematogaster* with 56 morphospecies (12.79%). In contrast, within the leaf litter habitat, *Pheidole* demonstrated the greatest morphospecies richness, with 35 morphospecies (10.93%), followed by *Strumigeny*s (26 morphospecies; 8.13%) and *Crematogast*er (20 morphospecies; 6.25%).

Temporal trends revealed distinct shifts in genus-level richness across sampling years. In 2011, *Camponotus* had the highest number of canopy morphospecies, with 29 (12.80%). However, in subsequent years, *Polyrhachis* emerged as the most morphospecies-rich genus in the canopy, with 23 morphospecies (12.79%) in 2015 and a substantial increase to 52 morphospecies (23.00%) in 2019. Within the leaf litter, *Strumigeny*s was the most morphospecies-rich genus in 2011 and 2015, with 13 (11.50%) and 11 (7.91%) morphospecies, respectively. By 2019, *Pheidole* had become the dominant genus in terms of morphospecies richness in the leaf litter, recording 30 morphospecies and representing 13.36% of the total.

Ant Community Similarity Patterns

Non-metric multidimensional scaling (NMDS) analysis of ant community composition revealed a distinct separation between canopy and leaf-litter habitats (NMDS stress = 0.12; Figure 6). Canopy plots clustered tightly on the left side of the ordination, while leaf-litter habitats occupied the right side, indicating that habitat type is a dominant driver of ant assemblage structure. Meanwhile OP stay in their own group, separated far from other habitat types. This suggests that ant communities in oil palm plantation are compositionally very different on structural complexity, resource availability and microhabitat compare to other habitat were invited the species in that area.

Overlay of species vectors identified several taxa strongly associated with particular habitat types. Canopy-associated taxa included *Crematogaster, Camponotus, Plagiolepis*, and *Tapinoma* all exhibiting long vectors pointing towards the canopy cluster. Conversely, *Acanthomyrmex, Hypoponera, Gesomyrmex, Solenopsis*, and *Secostruma* were strongly tied to leaf-litter habitats, as indicated by their vectors pointing towards the right-hand cluster. The vector lengths suggest these species contribute substantially to the observed variation among community assemblages. Like *Paraparatrechina* has strong associated to oil palm canopy meanwhile, *Mayriella* and *Rotastruma* strong associated to oil palm leaf litter (Figure 6).

Minimal separation among samples by sampling year (2011, 2015, 2019) was observed, indicating that temporal variation in community composition was less pronounced than differences attributable to habitat. Overall, the NMDS results suggest that sub-habitat type (canopy and leaf litter) is a stronger determinant of ant community structure than temporal variation across the sampling years.

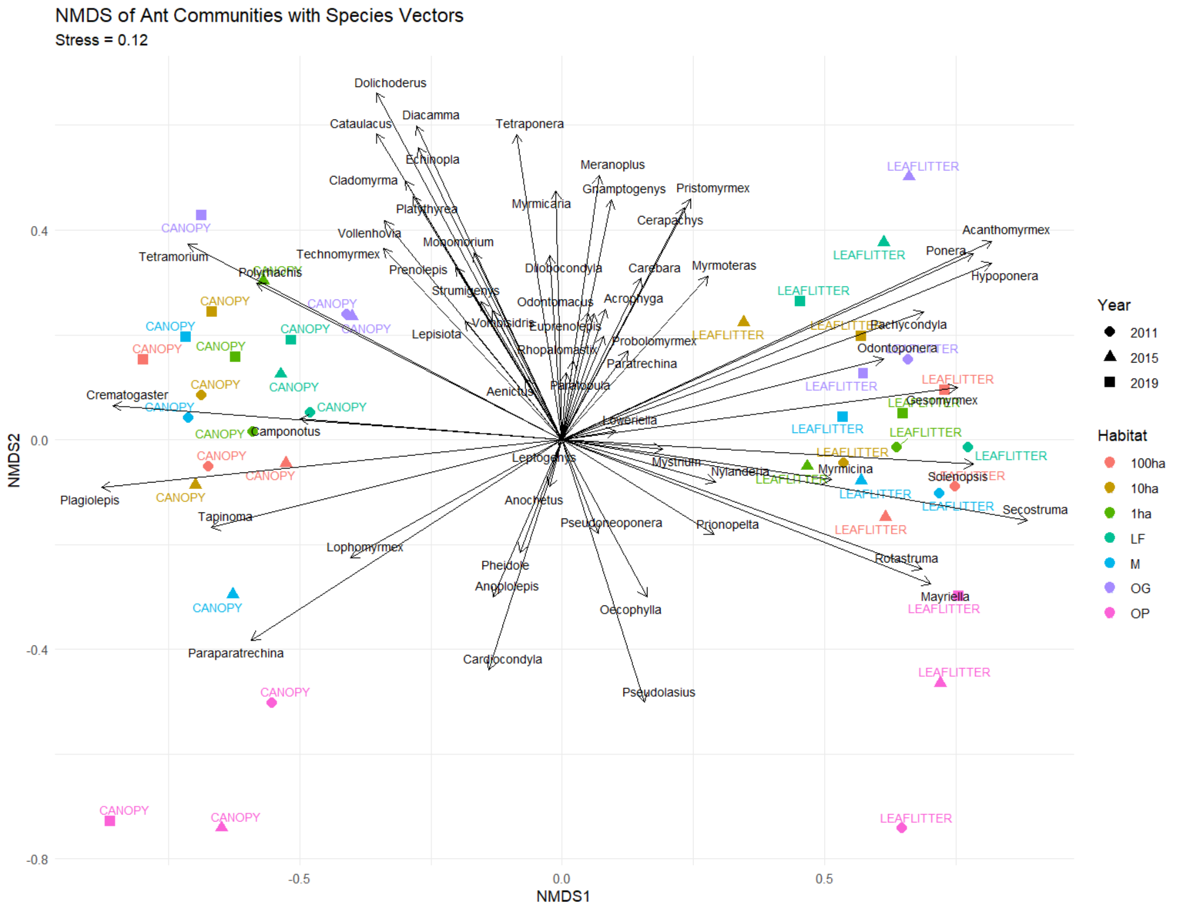


Figure 6. NMDS for ant communities in the canopy and leaf litter with different habitat types and years

DISCUSSION

Ant Community Composition and Dominance Patterns Over Time

Our three-year study, encompassing pre-fragmentation (2011), four years post-fragmentation (2015), and eight years post-fragmentation (2019) data from 68 consistent sample sites, successfully collected 106,084 individual ants representing 569 morphospecies. Consistent with broader Bornean ant species patterns (Pfeiffer et al. 2011), Formicinae and Myrmicinae emerged as the dominant subfamilies. Our findings on morphospecies richness largely align with Pfeiffer et al. (2011), who identified *Polyrhachis, Strumigenys, Pheidole, Camponotus,* and *Crematogaster* as prominent genera in Borneo. In our study, *Polyrhachis* consistently demonstrated the highest morphospecies richness, particularly in the canopy followed by *Camponotus* and *Crematogaster.* Within the leaf litter, *Pheidole*, *Strumigenys* and *Crematogaster* exhibited the highest richness (Figure 5). This sustained dominance of *Polyrhachis, Camponotus,* and *Crematogaster* in the canopy, and *Strumigenys* and *Pheidole* in the leaf litter, highlights their significant ecological roles in Bornean ant communities.

However, our observations on ant abundance contrasted with prior Sabah studies by Weiser et al. (2010), which reported higher counts for *Pheidole, Camponotus*, and *Crematogaster*. In our dataset, *Plagiolepis* was the most abundant genus across all three years, especially in the canopy, followed by *Crematogaster*. In the leaf litter, *Carebara*, *Strumigenys*, and *Pheidole* were the most numerous. The unprecedented high abundance of *Plagiolepis* in our study, relative to previous Sabah records (Brühl et al. 2003; Fayle et al. 2011; Luke et al. 2014; Pfeiffer et al. 2008), warrants further investigation. While it could suggest an increase in invasive species, *Plagiolepis* may also be a naturally dominant local species resilient to disturbance. Although Luke et al. (2014) identified *Plagiolepis* as an alien species from India, they did not classify it as invasive, and some sources even categorize it as a 'tramp species' (Seifert 2020). While invasive species are a concern due to their potential to displace native species and compromise ecosystem function (Gentili et al. 2021). Meanwhile, *Plagiolepis* has been observed in disturbed areas without necessarily disrupting native ecosystems (Klimes et al. 2015; Wittman 2014). Our data confirm *Plagiolepis*'s high abundance in disturbed habitats, including forest fragments (100-ha, 10-ha, 1-ha), logged forests, and oil palm plantations (Asmah et al. 2023). Conversely, *Crematogaster* was most abundant in the matrix and 1-ha areas, aligning with its role as a pioneer species well-adapted to newly opened and disturbed environments (Triyogo et al. 2020).

Temporal Dynamics of Ant Abundance and Richness in Fragmented Landscapes

Our analysis revealed significant temporal shifts in ant abundance over the eight-year study period. Canopy ant abundance was significantly higher in 2011 (pre-fragmentation) compared to both 2015 and 2019, suggesting their susceptibility to the immediate and medium-term impacts of land-use transformation. This vulnerability stems from their reliance on arboreal resources (Queiroz et al. 2013), which are directly affected by tree isolation, fragmentation, and reduced food availability post-clearing (Ahuatzin et al. 2019). Colony capacity, dependent on abundant and safe food sources (Antoniazzi et al. 2020), is also compromised. The reduced forest density and altered vegetation structure following clearing directly diminish food sources for canopy ants. Furthermore, increased canopy openness can affect ground temperatures and reduce soil biomass (Nazarreta et al. 2020), impacting nutrient cycling crucial for canopy ant colony development (Sanders et al. 2017). Extreme temperatures can restrict foraging activity (Parr & Bishop 2022), further affecting their presence.

In contrast to the declining canopy ant populations, leaf-litter ant abundance increased notably by 2019, eight years after habitat fragmentation. This rise was particularly evident in disturbed areas, such as logged forests and small forest fragments. These findings align with previous studies by Luke et al. (2014) and Hernández-Flores et al. (2020), which observed that certain ant groups, such as those in the Dolichoderinae subfamily, are highly adaptable to disturbed or altered environments. One possible explanation is that moderately disturbed habitats, like selectively logged forests or fragmented forest patches, often provide new microhabitats and nesting resources beneficial to leaf-litter ants. For example, fallen logs, deadwood, and decomposing organic material, which increase after disturbances, offer ideal nesting sites and foraging grounds (Didham 1997; Vasconcelos 1999). These conditions may favor generalist or disturbance-tolerant species, enabling them to thrive and even increase in abundance where more sensitive species may decline.

Both forest fragmentation duration and habitat significantly influenced ant morphospecies richness. Canopy and leaf-litter ant morphospecies richness both declined after four years of fragmentation and land change (2015). This pattern is potentially linked to the 2015-2016 El Niño event (Wigneron et al. 2020). The associated drought conditions and increased terrestrial temperatures (Pandey et al. 2019) would have stressed these ectothermic insects (Hethcoat et al. 2019), leading to reduced foraging and potential population declines (Goldman et al. 2020; Parr & Bishop 2022). Drought-induced changes in forest structure, increased leaf litterfall, and reduced tree nutrient availability (Gely et al. 2022; Nunes et al. 2021) likely contributed to this richness decline. However, larger canopy ant species, such as

Polyrhachis and *Camponotu*s, may exhibit greater resilience to heat (Kaspari et al. 2014). This is consistent with *Polyrhachis*'s high morphospecies richness in our study and its adaptable habitat use (Mezger & Moreau 2016). Conversely, the leaf-litter ant community showed a significant increase in species richness eight years post-land-use change. This rebound is likely driven by the increased leaf litter accumulation resulting from the 2015-2016 El Niño, providing an amplified food source and facilitating re-colonization (Nunes et al. 2021; Queiroz et al. 2013).

Ultimately, our investigation into ant communities across an eight-year fragmentation gradient underscores the dynamic and often contrasting responses of different ant functional groups to human-induced landscape change. The initial decline in canopy ant abundance and richness points to their immediate sensitivity, particularly when compounded by extreme climatic events. Conversely, the eventual increase in leaf-litter ant abundance and richness in disturbed areas suggests a resilience among certain groups, likely facilitated by altered habitat structures. These findings emphasize that habitat degradation can lead to biotic homogenization and a likely loss of specialist species in intensely modified landscapes, such as oil palm plantations, underscoring the critical need for conservation strategies that consider both the immediate and long-term consequences of land-use transformation on biodiversity.

Land-Use Specific Impacts on Ant Community Composition and Ecological Function

Our findings demonstrate that ant morphospecies richness is also directly influenced by land-use type. Oil palm plantations consistently showed lower canopy ant morphospecies richness compared to other land uses, supporting previous observations (Brühl & Eltz 2010; Fayle et al. 2010). This is likely due to the homogenous tree composition of these monocultures, which favor only a limited set of specialized or adaptable species, such as *Oecophylla smaragdina* (Piere et al. 2023) and certain invasive species like *Anoplolepis gracilipes* (Konopik et al. 2014). *Crematogaster* were notably abundant in fragment areas aligning with their preference for open canopy habitats (Triyogo et al. 2020) and their mutualistic relationships with pioneer trees like Macaranga (Putri et al. 2016), suggesting their adaptability to these modified landscapes. Some studies have also reported that a few *Crematogaster* species exhibit invasive characteristics (Stukalyuk et al. 2021). In contrast, *Paraparatrechine* were detect high composition with canopy oil palm, with also detected this species prefer in clearing forest areas due its preference in rotten areas (LaPolla et al. 2010). For leaf-litter ants, *Strumigenys* was highly abundant in 100-ha fragments and oil palm plantations, reflecting their predatory nature and preference for disturbed, open forests (Tang et al. 2019). *Pheidole* was prevalent across 10-ha, 1-ha, matrix, and old-growth forest areas, indicating their adaptability to various open habitats (Economo et al. 2015).

While overall ant abundance across canopy and leaf litter did not appear significantly affected by land-use changes in our specific analyses, as also noted by Denmead (2016), this apparent stability in total abundance can mask critical underlying shifts in species composition. The observed changes in dominant genera and richness for specific ecological guilds (e.g., *Plagiolepis* replacing *Crematogaster* dominance in disturbed canopies) highlight a potential long-term functional erosion within the ant community. For instance, the decline of mutualistic species like *Crematogaster*, which are vital for host-tree interactions (Fayle et al. 2011), suggests that even if overall ant numbers remain stable, the ecosystem services provided by the original ant community may be diminishing. This loss of specialized, endemic species and their unique ecological functions can ultimately lead to a localized reduction in ecosystem functionality, emphasizing that land-use change's impact extends beyond mere changes in abundance to profound alterations in community structure and ecological roles.

CONCLUSIONS

In summary, our findings underscore that fragmentation and land-use change cause persistent and complex alterations to ant communities. These effects are habitat-specific, taxon-specific, and time-dependent. While some resilience is observed, particularly in leaf-litter ants, the reduction in canopy ant richness and shifts in dominant genera highlight long-term ecological consequences. Without interventions to preserve forest heterogeneity and connectivity, we risk losing vital ecosystem functions provided by ants, especially in tropical systems like Borneo.

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AUTHORS DECLARATION

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Conflict of Interest

The authors declare no competing interests. The authors have no conflicts of interest to declare that are relevant to the content of this article.

Ethics Declarations

No ethical issue required for this research.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the supplementary materials**.**

Author Contributions

Asmah Siti was responsible for the conceptualization, methodology, investigation, data curation, formal analysis, visualization, project administration, and funding acquisition for this study, as well as preparing the original draft of the manuscript. Chen Lin Soo provided co-supervision and contributed to the writing, review, and editing of the manuscript. Kalsum M. Yusah, as the main supervisor, contributed to the overall supervision of the project, including conceptualization, methodology development, project administration, and critical review of the manuscript.

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