

Brief Report

Scale-Dependent Spatial Ecology of Paleotropical Leaf Litter Ants (Hymenoptera: Formicidae)

Lillian Germeroth ^{1,2}, Theodore Sumnicht ¹ and Robin Verble ^{1,*}¹ Department of Biological Sciences, Missouri University of Science and Technology, Rolla, MO 65409, USA² Huck Institutes of the Life Sciences, Pennsylvania State University, State College, PA 16802, USA

* Correspondence: verbler@mst.edu

Abstract: The grain for which an observer conducts a study is an important determinant of its outcome. Studies of ants have considered spatial grains spanning from single meters to entire forest ecosystems and found patterns related to nutrient availability, leaf litter depth, disturbance, and forest composition. Here, we examine a Bornean leaf litter ant community at small (1–4 m) and large (50–250 m) spatial scales and consider the differences in community structure using structured 1 m² quadrats sampled via leaf litter sifting and Berlese extraction. We found that small-scale patterns in ant abundance and richness did not spatially autocorrelate within a plot until >1.5 m. Leaf litter characteristics, forest stand characteristics and sampling season were homogenous among our sites, suggesting that macro-scale stand variables are not largely regulating the small spatial scale ant communities: These may be driven by microclimate, competition, niche space, nutrient available, microclimatic conditions, or other localized effects. Further experimental work is needed to elicit causal mechanisms.

Keywords: tropical conservation; biodiversity; semivariogram; Borneo; Sabah; Malaysia; UNESCO man and biosphere reserve



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1. Introduction

Environmental gradients and spatial dynamics influence species distributions and community composition at multiple scales [1], and “ecological patterns and processes are characteristically scale-dependent” [2]. Gradients in temperature and elevation [3], climate [4], abundance of sympatric colonies [5], and disturbance [6] shape ant metacommunities (metacommunity = set of interacting communities connected by dispersing species [7]) at various scales. However, ant metacommunity dynamics are most commonly examined at forest-stand or site scales and less commonly at small scales, despite known high variation in abundance and species richness at the small scale, and despite the fact that environmental heterogeneity at both the local and landscape scale structures local ant communities [8]. Supporting this, Kaspari found that densities of litter ants vary 10–20-fold at the 1-m² scale in neotropical forests [9].

Ant species appear to distribute randomly across vertical environmental gradients in tropical forests; however, abundant species segregate into patchy mosaics [10]. Ant mosaics occur when competition between species results in patchworks of mutually exclusive territories: Ant mosaics are documented in tropical forest canopies [11], but less evidence exists for high interspecific competition in leaf litter ants [12]. Thus, resource availability, not competition, is thought to be the likely driver of tropical leaf litter metacommunities [9,13]. Patchy distribution of ground-dwelling ants [13,14] may be explained by leaf litter physical (e.g., moisture, leaf shape, temperature) or chemical (e.g., compounds present in leaf tissues, state of decomposition) characteristics, local topography [15], resource availability [15,16], and vegetation structure and composition [17]. Theunis and colleagues found that leaf litter ant species distribution shows a periodic spatial structure related to interspecific

competition at small scales (<10 m), but that at larger scales (>50 m), environmental factors aggregated colonies of species that responded favorably to those factors [12]. The small-scale patterns that drive ant diversity may have large implications for the larger ecosystem, since leaf litter ants comprise 45–50% of all leaf litter macroinvertebrates [18] and engage with their environment at multiple trophic levels [19].

The grain at which observations are made for an ecological study has the potential to influence its outcome. While other studies [12,15] have considered spatial questions of grain (the finest level of spatial detail observable [20]) and extent (maximum area of consideration [20]), we found no literature that addressed the smallest spatial scales (immediate adjacency) of variance, despite its importance for overall community structure and dynamics. Herein, we examined patterns in spatial distribution and variance of ant communities at the 1 m (small) and >50 m (large) scales. Specifically, we examined the effect of distance on the composition, similarity, and richness of ant communities across short (1–4 m) and long (50 m) distances.

2. Materials and Methods

2.1. Study Site

Sampling was conducted from June to July 2019 at the Crocker Range Biosphere Reserve, Sabah, Malaysian Borneo (5°51′23.9″ N, 116°08′15.9″ E). The Crocker Range Biosphere Reserve was designated an UNESCO Man and Biosphere (MAB) Reserve in 2014. MAB sites are characterized by three protection zones: core, buffer, and transition. Core areas (144,492 hectares) are those in which very limited human activities are permitted, ecotourism is restricted, and forest product harvesting is forbidden. Buffer areas (60,313 hectares) are those areas that protect core forest reserves from encroachment by transitional and agricultural sites. Buffer forests allow higher rates of ecotourism and limited harvesting of forest products. Transition sites are agriculturally developed and human-inhabited. The land use types in these areas do not support comparisons with core and buffer forests for leaf litter arthropods; thus, they were excluded from this analysis. The Crocker Range core and buffer forests are home to approximately 400 distinct ecological communities. We restricted the spatial extent of our sites to minimize sampling multiple forest communities. A complete description of the study area can be found in Yoh et al., (2020) [21].

2.2. Field Methods

We sampled leaf litter ant communities at twelve forest plots (six core sites, six buffer sites) in June and July 2019 (dry season). Each plot was characterized by percent canopy cover, canopy height, size of largest local trees (cm, height, and circumference at breast height, then converted to diameter at breast height), distance among trees, size of largest rotting logs (cm, circumference), abundance and size class of lianas, and abundance and size class of standing vegetation. Each plot was separated by >50 m and consisted of 16 (1 m × 1 m) quadrats ($n = 192$ quadrats). Quadrats were placed immediately adjacent to one another such that all 16 quadrats were contained in a 4 m × 4 m grid (16 m²). Plot locations were chosen randomly with consideration of sampling ease (Figure 1).

Ants were sampled within each plot between 10:00–16:00 h in fair weather using Berlese extraction [22]. All quadrats within a plot were sampled a single time on a given day for a total of 192 samples. Quadrat sampling order and sampler were haphazardly selected. Leaf litter depth was measured to the nearest 1 cm by inserting a wire vertically through the litter to mineral soil at four haphazardly selected locations within each quadrat. Leaf litter depth was then averaged for each individual quadrat. We collected all leaf litter and biological material within a plot down to mineral soil and separated the coarse material from the fine leaf fragments and arthropods in a 1 cm mesh litter sifter [23]. Siftate was stored in linen bags for <4 h, then placed in passive hanging Berlese funnels for 48 h.

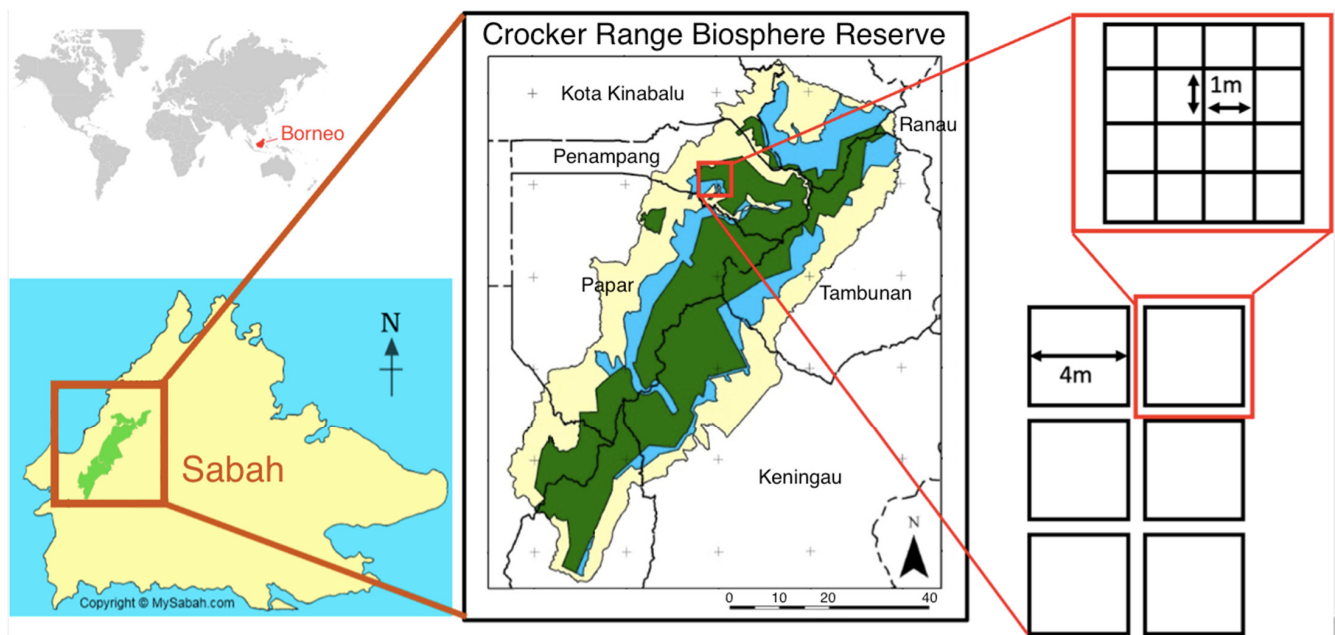


Figure 1. Location of study site within the Crocker Range Biosphere Reserve, Sabah, Malaysia. The study site encompasses both the core and buffer forest (green and blue respectively; center panel). Within each of the core and buffer zones, six 16 m² plots were established with 16–1 m² quadrats within for a total of 12 plots and 192 quadrats.

Collected ants were stored in 70% ethanol, sorted, counted, pointed, and identified to genus using published global and regional keys [24–26]. Identifying to genus served as the most efficient way to assess community composition and ecological patterns [27]. Voucher specimens were deposited in the entomological collection at the Institute for Tropical Biology and Conservation at the Universiti Malaysia Sabah, Kota Kinabalu.

2.3. Data Analysis

We calculated Jaccard similarity coefficients among all quadrats and among quadrats within plots as a measurement of evenness and measured quadrat distance as a continuous variable representing linear distance between individual pairs of quadrat centers. We compared evenness among quadrats nested within plots using a least squares model. We compared evenness, genus richness, and abundance among plots using a standard least squares model. We compared differences (the absolute value of the difference between values) in genus richness and ant abundance among quadrat distances within plots using a nested least squares model. We used a standard least squares model to test the effects of litter depth and its interaction with plots on ant genus richness and abundance (independent of one another).

We applied uniformity tests to quadrats within plots to compare community metrics among quadrats within plots. We used mixed models to examine the effect of quadrat position within plots on leaf litter depth, ant abundance, and ant genus richness. We used a spatial repeated structure and fit six spatial models (spherical, Gaussian, exponential, power, and best fit with anisotropic and nugget effects) to our data. The best fit model was selected comparing AICc among all plots and selecting the lowest values. We generated semivariograms by plotting distance (x) against semivariance (y) for ant abundance and ant genus richness for all quadrats within plots and averaged semivariance, sill, range, and nugget among quadrats resulting in mean values with standard errors for each plot. We visualized genus-level abundance and richness using a heat map where red represents higher abundance and green represents lower abundance. Abundance categories are consistent among genera to allow for inter-genus comparisons. Finally, we visualized Shannon diversity across all local-scale plots using the same heat map.

We regressed relevant community metrics against leaf litter depth and leaf litter surface temperature independently and calculated linear fit using R^2 values. We also regressed ant abundance and genus richness and calculated fit using an R^2 value. We calculated relative abundance for all genera and subfamilies as the number of individuals counted in that genus or subfamily divided by the total number of ants collected.

Forest plot characteristics were compared among plots using multivariate analyses of variance (MANOVA, $\alpha = 0.05$). Cumulative ant genus richness was compared between core and buffer forest using incidence-based sample accumulation curves [28] generated by the program EstimateS. The curves illustrate how the number of genera captured compares to the number of genera that are likely present at a site based on the number of new genera added per sample. All analyses were conducted in EstimateS [29], JMP 2019, SAS 2019, and Excel (Microsoft Office 2019).

3. Results

We collected a total of 20,657 ants representing 61 genera and 9 subfamilies during this study, representing approximately 95% of the genera present in the community based on estimates from sample accumulation curves (asymptote Core = 53, Buffer = 58; Figure 2). The number of ant genera found in a sample increased linearly with ant abundance across all samples ($n = 192$, $R^2 = 0.65$). Core forests housed 50 genera, and buffer forests were home to 54 genera; 42 genera were found in both zones (Table 1). We found no relationship between litter surface temperature and ant abundance ($R^2 < 0.01$) or ant genera richness ($R^2 = 0.03$). Leaf litter depth correlated with ant genera richness ($R^2 = 0.16$), but less with ant abundance ($R^2 = 0.05$). Ant genus richness and abundance correlated ($R^2 = 0.39$). Stand-level forest characteristics did not significantly vary among plots ($p > 0.05$ for all characteristics measured).

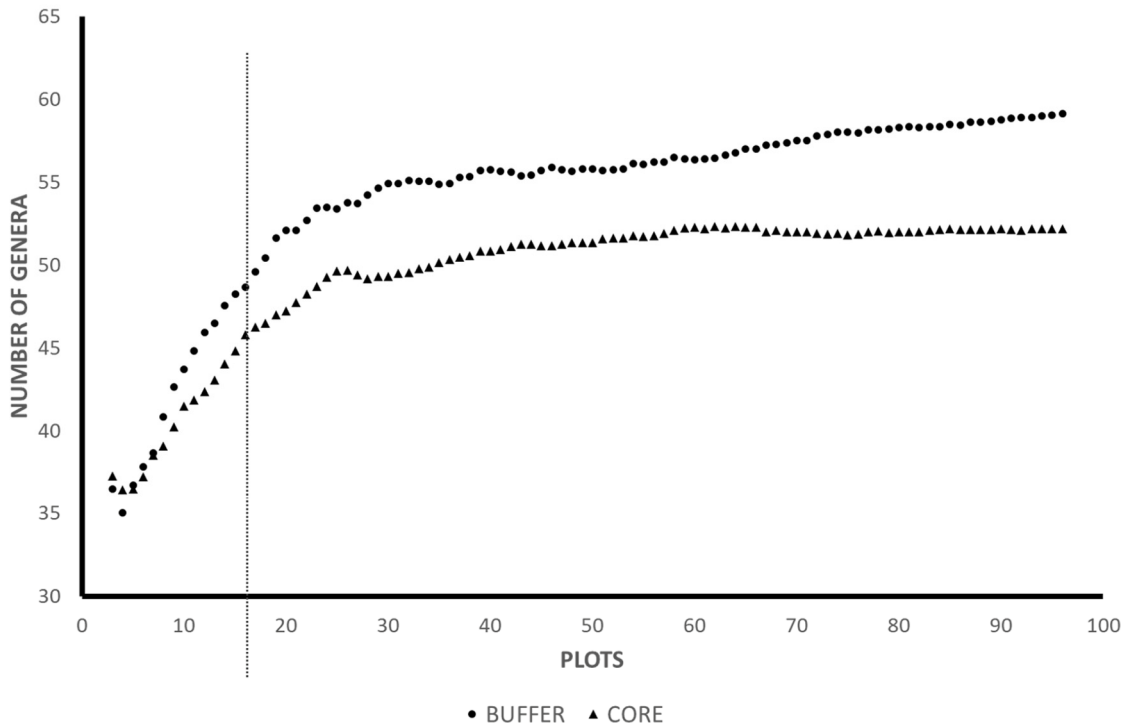


Figure 2. Genus accumulation curves for buffer and core forests. Our 16 plots capture approximately 95% of the genus-level ant diversity present in both core and buffer forests. Symbols represent the cumulative number of genera recorded as the cumulative number of plots increased.

Table 1. Relative abundance of all genera collected across all plots. RA = relative abundance. Values represented as proportions.

| Subfamily | Genus | Total Abundance | Genus RA | Subfamily RA | Genus Total Abundance Buffer | Genus Total Abundance Core |
|----------------|-------------------------|-----------------|----------|--------------|------------------------------|----------------------------|
| Amblyoponinae | <i>Mystrium</i> | 3 | <0.001 | 0.002 | 3 | 0 |
| | <i>Stigmatomma</i> | 41 | <0.001 | | 26 | 15 |
| Dolichoderinae | <i>Dolichoderus</i> | 2 | <0.001 | 0.063 | 0 | 2 |
| | <i>Loweriella</i> | 454 | 0.022 | | 409 | 45 |
| Dorylinae | <i>Aenictus</i> | 69 | 0.003 | 0.006 | 35 | 34 |
| | <i>Cerapachys</i> | 7 | <0.001 | | 7 | 0 |
| | <i>Lioponera</i> | 18 | <0.001 | | 0 | 18 |
| | <i>Parasyscia</i> | 26 | 0.001 | | 16 | 10 |
| Ectatomminae | <i>Gnamptogenys</i> | 14 | <0.001 | <0.001 | 4 | 10 |
| Formicinae | <i>Anaplolepis</i> | 2 | <0.001 | 0.140 | 1 | 1 |
| | <i>Camponotus</i> | 28 | 0.001 | | 15 | 13 |
| | <i>Colobopsis</i> | 2 | <0.001 | | 0 | 2 |
| | <i>Echinopla</i> | 2 | <0.001 | | 2 | 0 |
| | <i>Euprenolepis</i> | 2 | <0.001 | | 0 | 2 |
| | <i>Myrmoteras</i> | 167 | 0.008 | | 119 | 48 |
| | <i>Nylanderia</i> | 2486 | 0.120 | | 1939 | 547 |
| | <i>Paraparatrachina</i> | 13 | <0.001 | | 2 | 11 |
| | <i>Polyrachis</i> | 6 | <0.001 | | 1 | 5 |
| | <i>Prenolepis</i> | 93 | 0.004 | | 93 | 0 |
| | <i>Pseudolasius</i> | 29 | 0.001 | | 29 | 0 |
| Leptanillinae | <i>Leptanilla</i> | 2 | <0.001 | <0.001 | 0 | 2 |
| Myrmicinae | <i>Acanthomyrmex</i> | 60 | 0.003 | 0.695 | 25 | 35 |
| | <i>Calyptomyrmex</i> | 58 | 0.003 | | 29 | 29 |
| | <i>Cardiocondyla</i> | 34 | 0.002 | | 26 | 8 |
| | <i>Carebara</i> | 3537 | 0.171 | | 1683 | 1854 |
| | <i>Cataulacus</i> | 2 | <0.001 | | 2 | 0 |
| | <i>Crematogaster</i> | 50 | 0.002 | | 2 | 48 |
| | <i>Eurhopalothrix</i> | 12 | <0.001 | | 0 | 12 |
| | <i>Lophomyrmex</i> | 2932 | 0.142 | | 1347 | 1585 |
| | <i>Lordomyrma</i> | 13 | <0.001 | | 7 | 6 |
| | <i>Mayriella</i> | 322 | 0.016 | | 233 | 89 |
| | <i>Meranoplus</i> | 29 | 0.001 | | 25 | 4 |
| | <i>Monomorium</i> | 37 | 0.002 | | 37 | 0 |
| | <i>Myrmecina</i> | 114 | 0.006 | | 35 | 79 |
| | <i>Myrmecaria</i> | 309 | 0.015 | | 0 | 309 |
| | <i>Pheidole</i> | 4284 | 0.207 | | 2374 | 1910 |
| | <i>Pristomyrmex</i> | 65 | 0.003 | | 31 | 34 |
| | <i>Proatta</i> | 73 | 0.004 | | 73 | 0 |
| | <i>Solenopsis</i> | 77 | 0.004 | | 4 | 73 |
| | <i>Strumigenys</i> | 1154 | 0.056 | | 970 | 184 |
| | <i>Syllophopsis</i> | 81 | 0.004 | | 40 | 41 |
| | <i>Tetramorium</i> | 1018 | 0.049 | | 537 | 481 |
| | <i>Vollenhovia</i> | 92 | 0.004 | | 40 | 52 |
| | <i>Vombisidris</i> | 2 | <0.001 | | 0 | 2 |
| Ponerinae | <i>Anochetus</i> | 28 | 0.001 | 0.096 | 21 | 7 |
| | <i>Brachyponera</i> | 1235 | 0.060 | | 765 | 470 |
| | <i>Cryptopone</i> | 16 | <0.001 | | 12 | 4 |
| | <i>Diacamma</i> | 1 | <0.001 | | 1 | 0 |
| | <i>Ectomomyrmex</i> | 7 | <0.001 | | 3 | 4 |
| | <i>Emeryopone</i> | 1 | <0.001 | | 1 | 0 |
| | <i>Harpagnathos</i> | 2 | <0.001 | | 2 | 0 |

Table 1. Cont.

| Subfamily | Genus | Total Abundance | Genus RA | Subfamily RA | Genus Total Abundance Buffer | Genus Total Abundance Core |
|---------------|----------------------|-----------------|----------|--------------|------------------------------|----------------------------|
| Proceratiinae | <i>Hypoponera</i> | 424 | 0.021 | | 246 | 178 |
| | <i>Leptogenys</i> | 64 | 0.003 | | 44 | 20 |
| | <i>Mesoponera</i> | 1 | <0.001 | | 1 | 0 |
| | <i>Myopias</i> | 32 | 0.002 | | 26 | 6 |
| | <i>Odontomachus</i> | 51 | 0.002 | | 7 | 44 |
| | <i>Odontoponera</i> | 59 | 0.003 | | 39 | 20 |
| | <i>Ponera</i> | 52 | 0.003 | | 19 | 33 |
| | <i>Discothyrea</i> | 11 | <0.001 | <0.001 | 5 | 6 |
| | <i>Probolomyrmex</i> | 3 | <0.001 | | 1 | 2 |

We found no difference in genus richness between core and buffer forests ($p = 0.21$; mean genus richness per quadrat: core = 9.27, buffer = 9.87). Among quadrats nested within plots, we observed no difference in genus richness ($p = 0.1030$). We observed a difference in total ant abundance between core and buffer forests ($p = 0.008$, $MS = 39,016.5$, $F = 7.1875$, $p = 0.008$. Core mean = 93.3 ants per quadrat. Buffer mean = 123.18 ants per quadrat). We also observed differences in ant abundance among quadrats nested within plots ($F = 2.08$, $DF = 36$, $p = 0.0013$) and among plots ($p < 0.0001$, $MS = 51,913.5$, $F = 18.7129$, $p < 0.0001$. Range: 23.44–240.44, Figure S1).

Small Scale Spatial Ecology

Taxonomic similarity was highly variable among plots and quadrat distances nested within plots ($p < 0.0001$, $F = 5.16$, $DF = 11$) and showed no relationship to distance ($R^2 = 0.02$). Spatial spherical models showed best fit for distances between quadrats within plots. At short distances, quadrats did show spatial autocorrelation (mean range among all plots = 1.27 m, $SE = 0.109$; Table S1); however, for all plots, at distances greater than 1.5 m, quadrats were not spatially autocorrelated. There was no observable pattern in distance-decay of similarity within plots and no linear correlation between distance between plots and the similarity of ant assemblages (Jaccard similarity coefficient, $R^2 = 0.0207$).

4. Discussion

We found that ant genus richness was similar between core and buffer sites, and ant abundance varied between the two, with the highest ant abundance in buffer sites. Additionally, we found that small-scale patterns in ant abundance did not spatially autocorrelate. Thus, our results demonstrate that large-scale patterns in ant abundance may not mirror those at smaller spatial scales; however, both are predictably patchy [17].

The effects of large-scale forest disturbances on ant communities have been well characterized in tropical ecosystems [30–32]). Fewer studies have examined smaller-scale persistent disturbances, such as low impact trail systems or long-term research plots such as those present in the MAB buffer zones, and their impacts on ant communities. The small-scale studies that do exist generally find negative associations (e.g., Mohamed et al., 2019, hiking trails [33]; Barber 2015, hiking trails [34]) or no effect (Kwon 2015, roads [35]). Ant abundance can respond positively to human presence [36], possibly because of novel or more abundant resources, which may help explain the increase in ant abundance observed in this study. Known drivers of semi-local (<10 m scale) ant distribution and abundance patterns include land use patterns [37], leaf litter characteristics [38], seasonal trends [39], forest stand characteristics, and resource availability [40].

Leaf litter characteristics, forest stand characteristics and sampling season were homogenous among our sites, suggesting that macro-scale stand variables are not largely regulating the small spatial scale ant communities: These may be driven by microclimate, competition, niche space, nutrient availability, microclimatic conditions, or other localized effects. Very less is known about how communities function at this scale; however, work

by Xing et al., (2022) [41] found that ant species turnover is higher in horizontal space than in vertical space. While these effects can be species-specific [42], we observed that the total ant abundance decayed rapidly with distance (Figures 3 and 4).

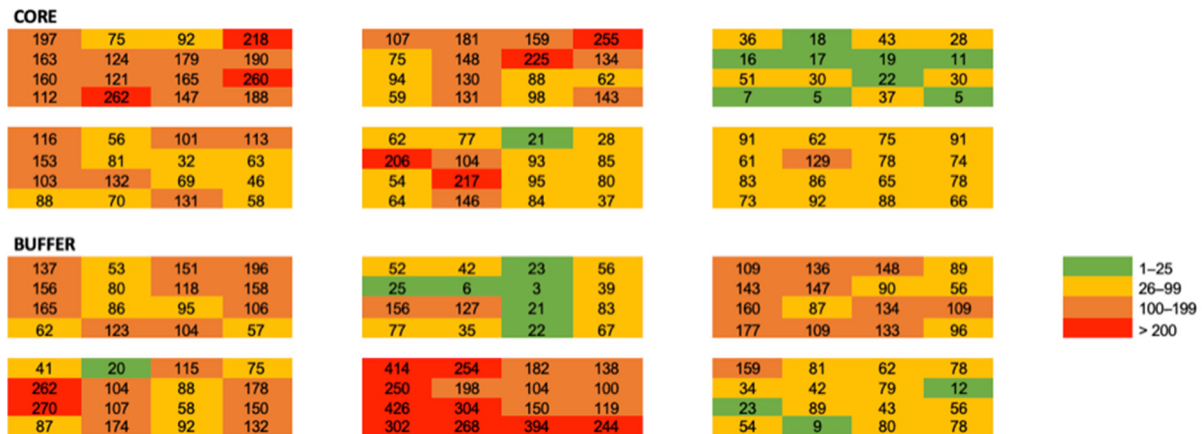


Figure 3. Heat map of total ant abundance among all plots and quadrats.

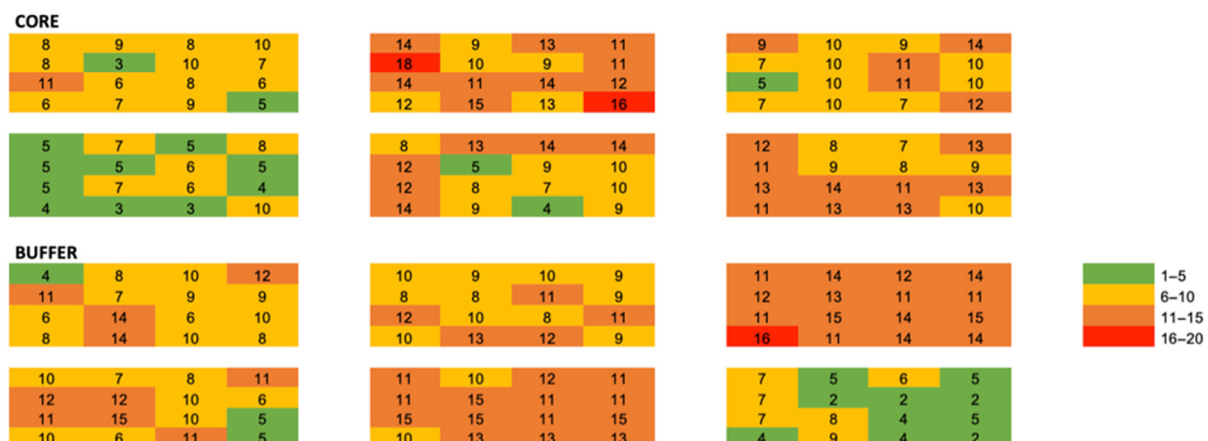


Figure 4. Heat map of genus richness among all quadrats and plots. Values are absolute richness per quadrat.

Within a subfamily, we observed multiple genera that were often found in only core and only buffer forests (Table 1). In particular, *Strumigenys*, *Nylanderia*, and *Loweriella* were highly abundant in buffer forests as compared to core forests. The genus *Nylanderia* is known from a single species in Borneo (*N. kraepelini* Forel, 1905) [43], but is a well-known invader in other systems [44]. Likewise, *Loweriella* is a monotypic genus found only in Borneo (*L. boltoni* Shattuck, 1992). A study by Rubiana et al., (2015) found that the genus occurred in disturbed forests [45]. Borneo is the epicenter of *Strumigenys* diversity with 97 recorded species, and the genus has at least 24 species that are known to occur outside their native range [46].

Locally rare genera were likely to be found in core forests than in buffer forests, and locally abundant genera were more likely to be found in the buffer forests. Rare species are the first to become locally extinct as a result of human disturbance [47]. We found locally rare species that occurred exclusively in both core and buffer forests. Our results may be a product of undersampling, high degrees of patchiness, or human disturbance in both zones. From a conservation management perspective, our study provides support for the continued application of zonation models in the Crocker Range MAB site. Given the similarity of the buffer and core forests, the high degree of overlap in genus composition, and the positive numerical response of ants to increased human presence, our study lends

support to this model as an effective way to maintain biodiversity in ant communities at MAB sites, and it provides support for the assertion that low impact human use of forests can coexist with sustainable models of biodiversity conservation, though caution is warranted in overextrapolation of this result. Our study is limited in its short sampling time and small sample size. We sampled a relatively small spatial area of the entire MAB reserve. Ant abundance has limitations in its usefulness as a metric of community diversity, given that ants are central-place foragers, and abundance can be skewed by nest location [2]. Nonetheless, abundance may be interpreted as a surrogate for local ant activity and provide important information about the site's nutrient and microclimatic conditions.

We encourage future studies in the region that continue to examine ant and leaf litter fauna in the Crocker Range, which is an understudied taxon in the region. Ecological, life history behavioral, and basic science studies are lacking for many of the ants known from the site. Future studies should also consider the impacts of large-scale forest management strategies for the MAB site and sustainable economic activities that can be created in the buffer zone.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15040494/s1>. Table S1: Spatial autocorrelation in ant abundance occurs at scales >1.5 m in all plots; Figure S1: Ant abundance (number of individuals) among all plots (16 m²). X = quadrat. Y = number of ants present. Sites connected by a letter are not significantly different (alpha = 0.05). Bars represent standard error.

Author Contributions: R.V. obtained financial support. R.V. and T.S. designed the project. R.V., T.S. and L.G. prepared project logistics and supplies. T.S. and L.G. conducted field data collection. L.G. and T.S. completed most ant identification. R.V. and L.G. performed data analysis. R.V. and L.G. wrote the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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