

Elevation and leaf litter interact in determining the structure of ant communities on a tropical mountain

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Abstract

Tropical mountains encompass a wide range of environmental conditions and are useful models for studying drivers of community structure. Invertebrate species richness and abundance show various elevational patterns. However, the drivers of these differences are not well understood, although microhabitat complexity is potentially important. We studied ground-dwelling ants using pitfall trapping and hand collection on Mt. Wilhelm (Papua New Guinea) from 169 to 3,795 m a. s. l. We tested for the effects of elevation and leaf litter depth (as a measure of microhabitat complexity) on ant abundance, species richness, and composition. We sampled 118 species, with ants present up to 2,331 m a. s. l. Species richness peaked at mid-elevation (~700 m), but the elevational pattern for abundance varied depending on sampling scale. Leaf litter depth negatively affected abundance once elevation had been accounted for, while elevation and litter depth had an interactive effect on species richness. Species richness was positively related to litter depth at lower elevations, but negatively above ~700 m. Species composition varied with elevation and less strongly with leaf litter depth. We speculate that in the lowlands, litter depth rather than temperature limits ant communities. At high elevations, the deeper litter decreases temperature of the litter layer, and temperature becomes limiting. At mid-elevations, temperature is not yet too low, and litter is still relatively deep, hence generating a mid-elevation peak in ant richness. Our results may explain differing richness-elevation patterns of litter arthropods around the world and provide testable predictions for future studies on this topic.

KEYWORDS

altitude, elevational gradient, Formicidae, microhabitat availability, mid-elevation peak, Papua New Guinea, rainforest, tropical mountains

1 | INTRODUCTION

The manner in which communities vary in relation to elevation is of broad interest to ecologists (McCain & Grytnes, 2010; Rahbek et al., 2019). Elevational gradients provide useful natural systems

to study macro-ecological and macro-evolutionary processes since they are analogous to latitudinal gradients in some aspects, but on a small geographic scale (Lach et al., 2010; Sanders & Rahbek, 2012). Therefore, elevational gradients can be used for the study of environmental changes, including those accruing due to variation in

temperature and ecosystem productivity. Even though invertebrate abundance and species richness usually decrease with increasing elevation, there is usually a rapid species turnover with elevation, leading to overall high species diversity along entire gradients (Graham et al., 2014; Merckx et al., 2015). These changes in arthropod communities along elevational gradients provide insights into the impacts of temperature, habitat structure, and resources on these communities (Peters et al., 2014, 2016; Rahbek et al., 2019). Globally, the highest densities of species (including those that are endemics) are found in rainforest-covered tropical mountain ranges, which are characterized by distinct elevational zones (Leponce et al., 2016; Rahbek et al., 2019). However, relatively few pristine forest gradients remain, since most are under increasing pressure from human activities (Merckx et al., 2015; Peters et al., 2019).

The patterns of abundance and species diversity along tropical mountain slopes vary greatly among mountain regions, as well as among animal and plant taxa (Colwell et al., 2016). Three most common patterns are found: monotonic decrease, low-elevational plateau, and a unimodal relationship with a mid-peak (see McCain & Grytnes, 2010). The mid-elevational peak in species diversity appears to be the most common (Colwell et al., 2016; Rahbek, 2005). Similar unimodal patterns are also seen in the relationship between primary productivity and elevation (see Kessler, 2000; Rahbek, 1997, 2005).

In tropical rainforests, leaf litter makes up most of the top humus layer of the soil, but its volume (i.e., depth and/or mass) varies significantly in time and space. This is because litter fall and decomposition rates are determined by multiple factors such as weather, seasonality, topography, soil condition and plant species distribution (Goma-Tchimbakala & Bernhard-Reversat, 2006; Laird-Hopkins et al., 2017; Röderstein et al., 2005; Sayer, 2006). The amount of plant litter (i.e., above and below ground litter consisting of decaying leaves and roots) at a site results from the balance between primary productivity and decomposition rate (Coleman & Crossley Jr, 1996; Röderstein et al., 2005). This litter is an important resource for ground and soil-dwelling invertebrates, since it provides microhabitats and food (Ashford et al., 2013; Hattenschwiler et al., 2005; Shik & Kaspari, 2010). In turn, ground-dwelling invertebrates play vital roles in litter and soil dynamics by facilitating nutrient cycling and litter decomposition, together with bacteria and fungi, and hence mediate the reduction of decomposing materials to smaller substrates (Hattenschwiler et al., 2005; Kattan et al., 2006; Takeda & Abe, 2001). Furthermore, litter is important not only as a food source, but for invertebrate predators and scavengers such as spiders, ants and predatory beetles, as shelter and a source of prey (McGlynn & Kirksey, 2000; Potapov et al., 2020; Tuma et al., 2020). Therefore, litter availability usually positively affects soil and litter invertebrate abundance and species richness (Grimbacher et al., 2018; Jacquemin et al., 2016; Mueller et al., 2016). However, experimental removal of a proportion of the litter has a relatively stronger (negative) effect on the litter and soil fauna compared to litter addition, whose effects are more difficult to predict (Ashford et al., 2013; Grimbacher et al., 2018; Sayer, 2006), indicating that other factors may be limiting in these communities.

Rate of leaf litter fall from plant matter above ground decreases with elevation (Kitayama & Aiba, 2002; Röderstein et al., 2005; Yang et al., 2007). In contrast, fine-root litter production (from plant matter below ground) increases with elevation, and hence partly compensates for the decreased leaf litter fall at the highest elevations of tropical mountain forests (Graefe et al., 2008; Röderstein et al., 2005). Furthermore, the litter mass and its nutrients depend not only on elevation but also on forest type (Richardson et al., 2005). Therefore, the litter availability on the ground in tropical mountains is affected by the interplay of multiple factors, including litter fall dynamics, decomposition rates, species composition of plants, fungi, bacteria and invertebrates, moisture changes across the seasons, and climate (Fujii et al., 2018; Marian et al., 2019; Röderstein et al., 2005). The variable contributions of these processes likely result in different litter patterns with elevation in each mountain region. For example, litter depth can show mid-elevational peaks (tropical forest in India (Sabu et al., 2008)), increases with elevation (the Andes (Marian et al., 2019), and Panama (Olson, 1994)), and decreases with elevation (Borneo (Brühl et al., 1999) and between low and higher elevations in Puerto Rico rainforests (Yang et al., 2007)).

The distribution of leaf litter invertebrates varies greatly along tropical elevational gradients and between different regions. For example, in Puerto Rico, leaf litter invertebrates show either a decrease in total arthropod species richness and biomass with elevation, or vary a little with elevation, depending on the forest type and its litter composition (Richardson et al., 2005). Leaf litter invertebrates in western Panama show a mid-elevation peak in the number of species for the majority of invertebrate groups (Olson, 1994). In general, most studies on leaf litter invertebrates find a decreasing trend or a mid-peak with elevation (Longino & Branstetter, 2019; Marian et al., 2019). We hypothesize that these elevational patterns track the changes in resource availability, since there is a positive correlation of invertebrate abundance with forest floor litter mass (Yang et al., 2007). However, at present, it is not clear to what degree changes in leaf litter with elevation contribute to the variation in arthropod abundance and richness among studies.

We used ants as our focal insect taxon to test for the effects of elevation and leaf litter depth on insect communities. Ants were chosen as they are abundant and relatively diverse insects in leaf litter of tropical forests, play important ecological roles, and are good biological indicators of environmental changes (Agosti et al., 2000; Lach et al., 2010). As eusocial insects living in colonies, they are in particular sensitive to temperature and resource limitation (Lach et al., 2010). Previous studies that assessed the relationship between leaf litter depth or mass (i.e., surrogate for microhabitat availability and complexity) and ground-dwelling ants usually found positive effects (Grimbacher et al., 2018; Jacquemin et al., 2016) or no significant relationship (Donoso et al., 2010; Mann et al., 2018; Nakamura et al., 2009). However, these studies tested only for the effects of leaf litter variability at a single elevation. Overall, few studies of ground-dwelling ants along complete elevational gradients have measured both leaf litter depth (or mass) and the species richness of ant communities (Brühl et al., 1999;

Marathe et al., 2020; Olson, 1994; Sabu et al., 2008). Some of these found ant richness and leaf litter to peak at the same elevation, and they speculated that this pattern was driven by increased availability of prey and/or nesting niches (Brühl et al., 1999; Sabu et al., 2008). Similar hypotheses have been discussed in other studies of leaf litter ant communities over elevations that did not measure leaf litter volume (e.g. Longino et al., 2014). Yet, only one study has tested for the simultaneous effects of both elevation and leaf litter volume on the ant communities (Marathe et al., 2020). However, this did not test for an interaction between these drivers and considered only species richness. To date, we are not aware of any study assessing the interaction between the effects of elevation and leaf litter on ants, or indeed for any other invertebrate group.

Here, we investigated how elevation, leaf litter depth, and their interaction affect the abundance, species richness, and composition of ground-dwelling ants on Mt. Wilhelm (Papua New Guinea), one of the last tropical areas with intact forest ecosystems from the lowlands to the natural tree line (a complete elevational gradient, (Leponce et al., 2016)). This work represents the first study of the ground-dwelling ants on this tropical mountain, as previous studies focused on arboreal assemblages (Orivel et al., 2018; Plowman et al., 2017). We tested for the effects of elevation, leaf litter depth, and the interaction between these two variables on ant abundance and species richness. Based on previous studies (Brühl et al., 1999; Grimbacher et al., 2018; Sabu et al., 2008), we hypothesize that ant abundance and diversity will peak at sites with the thickest leaf litter layer due to higher microhabitat variability and availability (i.e., positive effects), potentially generating a mid-elevational peak at our sites (Colwell et al., 2016). Furthermore, we tested the simultaneous effects of elevation and leaf litter depth on ant species composition. We predict that species occurrences will vary with both elevation and leaf litter depth, but that elevation will be more important driver of abundance, species richness, and species turnover (Bishop et al., 2015; Brühl et al., 1999).

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted sampling along the Mt. Wilhelm elevational gradient located in Papua New Guinea (PNG). Mt. Wilhelm (4,509 m a.s.l.) is the highest peak of both the Bismarck range and of Papua New Guinea, with one of the highest rates of endemism and greatest diversities of insects and plants worldwide (Barthlott et al., 2007; Leponce et al., 2016). Undisturbed forest extends from the lowlands (~200 m a.s.l.) to the tree line (~3,700 m a.s.l.). We sampled in these undisturbed forests near eight field campsites (locations hereafter), spaced at ~500 m elevational intervals (Sam et al., 2019). Distance between the sampling locations varies, due to topography (41 km gradient with mean distance between neighboring locations of $5.87 \text{ km} \pm 2.69 \text{ SD}$, Figure S1). The mean annual temperature ranges from 27.4°C at 200 m a. s. l. to 8.4°C at the tree line (~3,700 m a.s.l.),

linearly decreasing with elevation at a rate of 0.54°C per 100 elevational meters (Leponce et al., 2016). Average annual rainfall ranges from 3,288 mm in the lowlands to 4,400 mm at 3,700 m a.s.l., with a distinct condensation zone between 2,500 and 2,700 m a.s.l. (Sam et al., 2019). Climate is perhumid, with relatively low seasonality. However, there is a drier period from June to September, while the rainfall is more variable in other months, and usually peaks in December and January (Leponce et al., 2016). For further details of localities and forest structure, see Leponce et al. (2016).

2.2 | Sampling methods

Sampling took place between October and November 2012 during an international expedition IBISCA New Guinea Our Planet Reviewed (Leponce et al., 2016). We used pitfall trapping and hand collection to assess the effect of elevation and leaf litter depth on ground-dwelling ant communities. Pitfall trapping is widely used to assess species diversity of surface-foraging ants (Gotelli & Colwell, 2001; Werenkraut et al., 2015). Ten pitfall traps were placed at 56 m intervals along a 560 m transect at each of the eight locations ($n = 80$; referred to as sites hereafter). Each transect tracked the elevational gradient topography (first site at the lowest elevation and the last in the highest within that location). Although the distance between sites within location is lower (from 56 m to 560 m) than between the locations (see above and Figure S1), we regard the sites independent for our focal insect group, where the same ant colonies in the litter are unlikely to be sampled over such a distance (McGlynn et al., 2003) and where each of the locations represented a typical forest for that elevational zone (Leponce et al., 2016). However, we are aware that our results relate only to the spatial scale and locations at which we sampled, and hence, we interpret our findings cautiously. Our design allows us to assess elevational differences across large (elevational locations) and small (pitfall sites) spatial scales in a challenging tropical mountainous area. The trap design follows Yusah et al. (2012). A 500 ml plastic bottle was taped to the end of a 19.5 cm diameter funnel filled with 72% ethanol and placed in an excavated hole, with the surface of the funnel leveled with the soil surface (Figure S2). Small roofs built over the funnels prevented falling leaf litter debris and rain from entering the funnels. Traps were collected after 72 hr.

Additionally, we conducted hand collection of ants at the pitfall trapping sites when the pitfall traps were taken out. This method was used to supplement the catches from pitfalls traps for fauna that might be under-sampled by traps (e.g. small cryptic species inside the leaf litter, soil, and slow-moving species). Ants were collected from forest floor leaf litter, dead wood, soil, and vegetation up to 2 m above ground level within a 2 m search radius from each pitfall trap. Hand collection was conducted for 15 min at each site by the same person (TMF). Leaf litter was spread on a white cloth sheet to help search for small ants from leaf litter and twigs. Sampling was conducted during days with minimal rain. Ants found using the two methods were stored in 2 ml vials with pure ethanol.

Although Winkler extraction method with a higher replication per site (≥ 20) is recommended to sample comprehensively the leaf litter ant fauna (Fisher, 1999; Longino & Branstetter, 2019; Marathe et al., 2020), our design combining pitfall trapping with hand collecting allowed rapid collection of samples during an expedition on which each location was visited for only three days. Species accumulation curves for different elevations did not cross, indicating that the elevational differences would be unlikely to change with more intensive sampling (Figure 1). Furthermore, similar species richness values (~ 50 on average) have been found in a lowland forest in PNG with using ten Winkler samples per site (Janda, 2007).

We measured leaf litter depth in cm (± 0.1 cm), at three points 30 cm from each pitfall trap, forming a triangle. Each value was measured by pushing a ruler in the leaf litter until it reached the soil surface, and the arithmetic mean of the three values was used as the estimate of the site leaf litter depth following Jacquemin et al. (2016). We considered in this study as "leaf litter" all the plant organic matter above the top layer of the compacted soil, mostly consisting of decaying and dry leaves, but partly of twigs and fine-roots (i.e., organic stand litter) (Katayama et al., 2013; Röderstein et al., 2005). We measured coordinates and elevation for each of the 80 pitfall sites along the gradient using a GPS unit (Garmin GPSMap 60CSx). Temperature was recorded every hour for the 72 hr in each of the locations using a data logger (Comet R3120) placed in the middle of each transect, and the arithmetic mean has been used for further analysis.

2.3 | Species identification

All specimens collected were sorted and identified to genera and then either to morphospecies or species level (hereafter referred to as

species, Table S1) using Bolton (1994), Shattuck (2000), the reference collection of PNG ants at the Institute of Entomology, Biology Centre of Czech Academy of Sciences and online databases (AntWeb, 2016; Janda, 2016). All wet and dry pinned specimens of each species (Accession Number: TMF001 – TMF0249) are deposited at the Institute of Entomology, Biology Centre of Czech Academy of Sciences.

2.4 | Statistical analysis

Sampling at the three highest locations did not yield any ants. However, we retained the lowest at which ants were not found ($\sim 2,700$ m a.s.l.) in our analyses. This is to reflect the full natural gradient for this insect group, as there were two species observed on the ground at 2,700 m at baits in another experiment (Moses J. pers. observ.), while minimizing issues relating to large numbers of zeroes for response variables. Hence, the top two locations without ants were excluded from the analyses (i.e., two locations of the six, with the corresponding 20 sites above 2,746 m a. s. l. removed). Queens and males were also excluded, with only workers being considered in all analyses, since these indicated presence of an established colony. Paired samples from pitfalls and hand collections were pooled and the resulting community data for individual sites were used for the statistical analyses conducted either at larger scale of locations ($n = 6$) or at smaller scale of individual sites, where leaf litter depth was also measured (total $n = 60$). All univariate analyses were performed in R version 3.6.0 (R Core Team, 2019), using Generalized Linear Models (GLM). We used the R packages "ggplot2" and "visreg" for plotting (Breheny & Burchett, 2017; Wickham, 2016). All multivariate analyses of species composition were conducted in CANOCO 5.04 (Ter Braak & Šmilauer, 2012a).

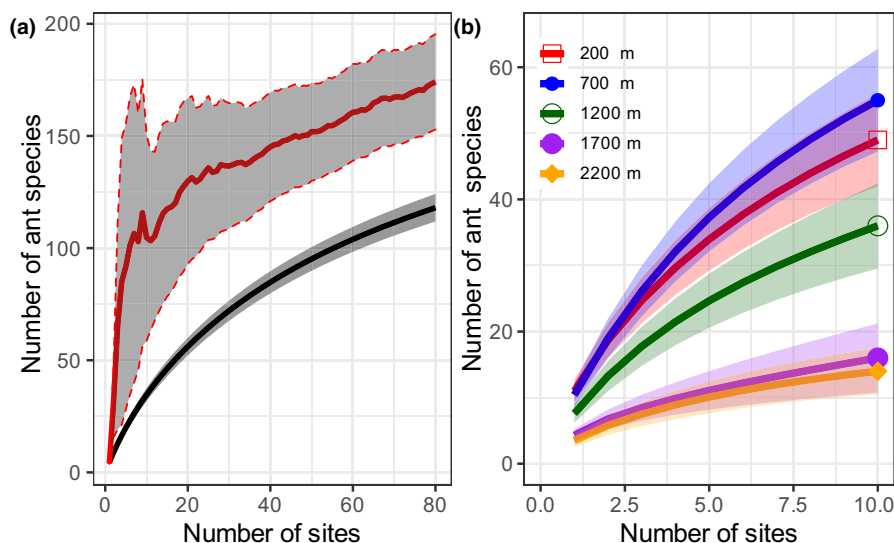


FIGURE 1 Accumulation curves of number of ant species with increasing number of sites sampled (a) for the whole Mt. Wilhelm elevational gradient ($n = 80$) using species-observed (black line) and Chao 2 functions (estimated total sp. richness = 174 mean ± 21.24 SD; red line with dashed boundaries), and (b) for each of the locations (eight research camps spaced by 500 m a.s.l., Figure S1). Curves were generated using sample-based incidence data. Solid lines are interpolations with 95% confidence intervals, and the points represent observed total species richness values. Only five of eight locations are plotted in (b) as no ants were found at the three highest locations (2,700–3,700 m a.s.l.)

First, we generated species accumulation curves for (a) the whole gradient (all sites as replicates) and (b) for each of the five elevational locations with ants separately (10 sites per location as replicates) and (c) for the same five locations but using sample coverage instead of the number of sites. We used the “iNEXT” package to calculate species accumulation curves based on incidence data (observed species diversity in sites \pm confidence intervals, generated using 999 bootstrap replications) (Chao et al., 2014; Chao & Jost, 2012; Hsieh et al., 2016). To estimate overall species richness of the ground-dwelling ant fauna targeted by our sampling methods at the whole gradient, we used the Chao 2 index from EstimateS version 9.1.0 software (Colwell, 2013). This allowed us to assess the representativeness of sampling for ant diversity between each of the five elevational locations where ants were present and for the whole gradient.

Prior to further analyses, we tested environmental predictors (i.e., elevation, leaf litter depth, and temperature) for multicollinearity using the *chart.Correlation* function in the R package “PerformanceAnalytics” (Figure S3). As the temperature was strongly negatively correlated with elevation (“Kendall’s” correlation coefficient $R_\tau = -0.80$) and showed similar effects on ant abundance and richness (Figure S4, Table S2), we present analyses including elevation but not temperature. In contrast, leaf litter depth was only weakly correlated with elevation and temperature ($R_\tau < -0.2$). This allowed us to test for the independent effects of leaf litter depth and elevation, and for the interaction between these two predictors. To do so, we used GLMs to assess the effects of elevation (continuous predictor in m), leaf litter depth (continuous predictor in cm), and their interaction on the number of ant workers per site (ant abundance) and number of ant species per site (species richness).

First, we ran a simple model including only elevation as a predictor to test for changes in abundance and richness (linear or quadratic, testing for the presence of a mid-peak at both the large (i.e., locations, $n = 6$) and small scales (sites, $n = 60$; see Tables S3 and S4) for comparability with previous studies conducted at larger scales (e.g. Fisher, 1999, 2004; Longino & Branstetter, 2019). We

used a Poisson distribution with a log-link function for each of the response ant variables (abundance and richness) as appropriate, since our data were positive counts and skewed. Three models (null model, linear (first-order polynomial) and non-linear (second-order polynomial; i.e., used to potentially detect a hump-shaped elevational pattern (Bishop et al., 2014; McCain & Grytnes, 2010)) were run for each response variable. Models were then compared using the change in corrected Akaike Information Criterion (ΔAICc) to select the most parsimonious model (lowest ΔAICc (see Burnham & Anderson, 2004)). Next, we tested the selected model using *dispersiontest* function from the “AER” package for overdispersion (dispersion value > 1). If required, we re-ran models using negative binomial error distributions, with the function *glm.nb* from the “MASS” package in R to account for overdispersion. The same protocol was repeated for the effects of only leaf litter depth on ant abundance and species richness. Finally, we constructed full models that included first- and second-order polynomial effects of both elevation and leaf litter depth, and their interactions (i.e., eight further tests for each of ant abundance and ant species richness, see Table S4 for details on all models). These were performed for each response variable and compared with the simple model based on elevation, using the same procedure (ΔAICc and overdispersion tests). We used the most parsimonious models for ant abundance and species richness and also tested the significance of the individual predictors (Murtaugh, 2014), using test of deviance at $\alpha = 0.05$, that is, a chi-square distribution-based test of Type I for the Poisson and negative binomial distributions “ANOVA (model, test = “Chisq)” (Table 1). For best models for abundance and species richness, we fit the tested predictions to the *ggplot2* charts using *predict.glm* function in R package “stats” with the following setting: *predict.glm(-model, newdata = dataframe, type = “response”, se.fit = TRUE)*. We also made predictions of changes in these values with elevation under the scenarios in which leaf litter depth was constant at either its observed minimum (0.43 cm), mean (2.72 cm), or maximum (7.50 cm) values along the analyzed gradient (i.e., across the 60 sites) using *predict.glm* function.

TABLE 1 Generalized linear models (GLMs) with analysis of deviance testing the effects of elevation and leaf litter depth on (a) the ant worker abundance (additive effect, $R^2 = .47$, Figure 4a) and (b) species richness (most complex model including interaction, $R^2 = .75$, Figure 4b,c) along the Mt. Wilhelm elevational gradient. Leaf litter depth¹ = effect of leaf litter depth fitted with first order polynomial. Elevation² = effect of elevation fitted with second-order polynomial. The results are for the best (most parsimonious) models that are chosen based on the lowest ΔAICc score and are used in Figure 4 (for all models and their AICc and R^2 comparisons see Table S4)

(a) Abundance	df	Deviance	Resid. df	Resid. deviance	p
Null (intercept)			59	128.83	
Elevation ²	2	53.43	57	75.40	<.001
Leaf litter depth ¹	1	7.03	56	68.37	.008
(b) Species richness	df	Deviance	Resid. df	Resid. deviance	p
Null (intercept)			59	252.16	
Elevation ²	2	177.36	57	74.80	<.001
Leaf litter depth ¹	1	0.43	56	74.37	.51
Elevation ² : Leaf litter depth ¹	2	10.56	54	63.80	.005

Finally, we assessed the effects of elevation and leaf litter depth on the ant species composition using multivariate canonical correspondence analysis (CCA, constrained ordination) (Ter Braak & Šmilauer, 2012b). Monte Carlo permutation tests (number of permutations = 999) were used to test for the significance of the effects of the environmental variables on the ant assemblages. A matrix of fifty samples (the highest three locations without ants were excluded) times species with data on worker abundances being log-transformed ($\log(n + 1)$) was used for the analysis. We excluded from analysis species that occurred only in a single site to account for the bias from rare species (68 species retained). Finally, we performed variation partitioning to assess the percentage of the variability in ant species composition explained by each of the two predictors individually (elevation and leaf litter depth) and by their overlap.

3 | RESULTS

We found a total of 118 ant species in 46 genera represented by 1,585 individual workers across the elevational gradient (Table S1). In the

first five elevational locations, each site yielded at least one ant species (max. 17 species), but there were no ants found in the last three locations above 2,331 m a.s.l. (i.e., 30 sites of 80 had no ants) (Figure 1b). In terms of the two sampling methods, hand collection yielded more species but a lower number of individuals (91 species, 472 individuals) than pitfalls (67 species, 1,113 individuals). The five most common species in terms of both number of collected individuals and number of occupied elevational sites (range > 1,500 m) were *Brachyponera croceicornis* (Emery, 1900), *Pseudolasius* cf. *breviceps* (Emery, 1887), *Rhytidoponera strigosa* (Emery, 1887), *Tetramorium* sp. 26 and *Carebara melanocephala* (Donisthorpe, 1948). The two most common species in the lowlands (<700 m) in terms of number of occupied sites were *Odontomachus simillimus* (Smith F., 1858) and *Nylanderia* aff. *vaga* (Forel, 1901), while the highest elevations (>1,200 m) were dominated by *Ancyridris* spp. and *Tetramorium* sp. 26 (Table S1).

Species accumulation across all elevations showed a gradual increase in ant richness with the curve not reaching an asymptote, with an estimated total species richness of 174 species (Chao 2 mean \pm 21.24 SD) (Figure 1a) and for each of the five locations (Figure 1b). Similar relative differences were found between individual locations either if half of sampling sites or half-sample coverage

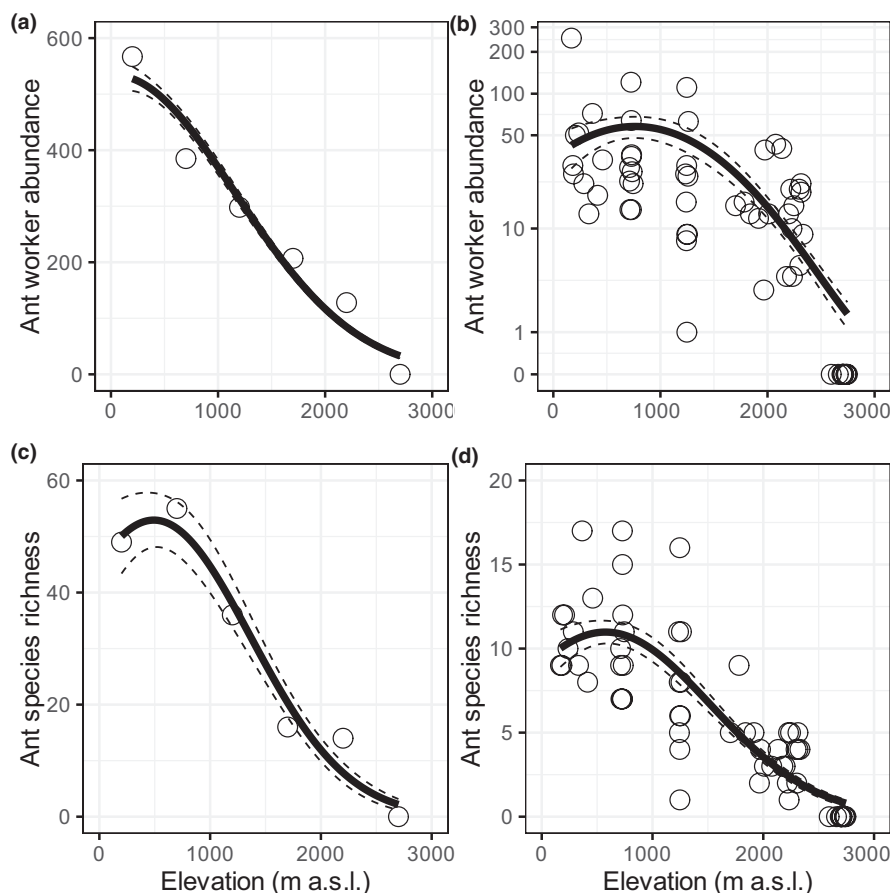


FIGURE 2 Relationships of worker ant abundance and ant species richness with increasing elevation on Mt. Wilhelm elevational gradient at different sampling scales. (a) and (c): patterns at the larger scale (total values across ten sampled sites spaced along a 560 m transect within each location, $n = 6$). (b) and (d): at the scale of individual sites ($n = 60$). Curves indicate fit with SE (dashed lines) using a GLM model with a second-order polynomial and Poisson (a–c) or negative binomial (d) distribution (see Table S3 and S4). The top two locations (above 2,700 m a.s.l.) without ants are excluded (see methods). Note the log-scale plotting is used in (b) for clarity as there are outliers

is considered (Figure 1, Figure S5). Interestingly, overall sampling completeness was then rather similar (~75%) for all locations (Figure S5). The highest observed richness across locations was at 700 m, followed by 200 m, 1,200 m, 1,700, and 2,200 m a.s.l.

Worker abundance showed significant near linear decrease with increasing elevation at larger scale ($\chi^2_{[2,3]}$, deviance = 839.8, $p < .001$) (Figure 2a), but a mild peak at ~ 800 m a. s. l. at the smaller scale of individual sites ($\chi^2_{[2,57]}$, deviance = 53.4, $p < .001$) (Figure 2b, Tables 1, S3 and S4). In contrast, species richness peaked at elevation ~ 700 m a. s. l. consistently at both spatial scales: large scale ($\chi^2_{[2,3]}$, deviance = 96.2, $p < .001$) and small scale ($\chi^2_{[2,57]}$, deviance = 177.4, $p < .001$) (Figure 2c,d, Table 1). If variance per location only is considered and elevational differences within transects are ignored, both mean abundance and species richness were slightly lower at 700 m a. s. l. than 200 m a.s.l. (Figure S6). However, note that this analysis ignores the elevational differences between our sampled sites within each location that varied up to 495 m a.s.l. (Figure S3), which were included in the full GLM models (Figures 2b,d, 3, 4). Leaf litter depth was positively related to ant richness ($\chi^2_{[2,57]}$, deviance = 16.8, $p < .001$) but not to ant abundance, where the null model performed better (Figure 3, Table S4). However, there was a negative effect of leaf litter depth on ant abundance when the leaf litter variation with elevation had been taken into account (a negative additive effect, Figure 4a, Table 1). This model predicted the lowest number of ant individuals at the observed maximum leaf litter depth. Furthermore, there was a significant interaction between the effects of elevation and leaf litter depth on the species richness (Table 1b). This model predicted the highest number of species at the low elevations with the highest leaf litter depth, with a linear decline with elevation for the highest leaf litter volumes but a unimodal relationship with elevation for medium and low leaf litter levels (Figure 4b,c).

Ant community composition varied significantly with both elevation and leaf litter depth (11% of the total species variation across the sites explained) (Figure 5a; CCA, pseudo- $F = 2.9$, $p < .001$). Elevation contributed a higher proportion of this variability (8%) compared to leaf litter depth (4%), and only 1% of variability overlapped between the two predictors (Figure 5b). The efficiency compared to unconstrained analyses (i.e., variance possible to explain by any predictors in the CCA) was high (89% for the first canonical axis, Figure 5a). A greater proportion of species showed preference for greater leaf litter depth at low elevations than at high elevations (Figure 5a). This trend could not be explained solely by the decrease of leaf litter depth with elevation, as this decline was rather small for the elevations at which ants occurred (up to 2,331 m a.s.l.; Figure S3).

4 | DISCUSSION

As expected, we found a positive correlation between leaf litter depth and species richness (Brühl et al., 1999; Sabu et al., 2008), although the relationship was not significant for ant abundance.

However, once elevation was included in our models, the impact of leaf litter on ant abundance became negative, while the positive effect on ant species richness persisted only at low elevations. This probably reflects a greater limitation of ground-dwelling ants by leaf litter availability at the lowest sites. This has been shown experimentally for beetles and ants in an Australian lowland rainforest where experimentally reduced litter layer decreased their abundances (Grimbacher et al., 2018). Overall, the effects of leaf litter on ant communities were much weaker than the effects of elevation. This was expected, because elevation is strongly correlated with temperature, the main abiotic driver of ant abundance and diversity over larger spatial and temporal scales (Arnan et al., 2018; Dunn et al., 2009; Tuma et al., 2020). Leaf litter availability is instead supposed to affect communities at local scales, over which it can be highly variable (Grimbacher et al., 2018; Jacquemin et al., 2016).

The evidence for a mid-elevation peak in species richness on the Mt. Wilhelm gradient conforms to patterns from previous studies of ground-dwelling ant communities (Bishop et al., 2014; Fisher, 1999; Longino & Branstetter, 2019; Longino et al., 2019; Longino & Colwell, 2011; Sanders, 2002; Szewczyk & McCain, 2016), although linear decreases have been also observed in some studies (e.g. Brühl et al., 1999; Fisher, 1996; Szewczyk & McCain, 2016). Analogous unimodal trends were found in our study in relation to temperature (Figure S4). Although elevation acts here as a surrogate for temperature, the prediction that this mid-peak is driven solely by leaf litter availability is not supported by our data. This is because leaf litter depth instead decreased monotonically with elevation in a similar manner to temperature, while the abundance and species richness were predicted to be the highest around 700 to 900 m a. s. l. for the lowest levels of leaf litter.

Notably, the relationship of ant abundance and richness with elevation varied and also depended on the spatial scale of the observations and the resolution of the elevational differences included in the models. The models indicated a slight mid-peak at 700 m a.s.l in the case of species richness at both large and small scales, while ant abundance decreased almost linearly at larger scale, or it showed a mildly unimodal change in the lowlands at smaller scale. Interestingly, a similar variation between relationships of abundance and richness with increasing elevation were found in Longino and Branstetter (2019). Although in that study such differences were more pronounced, that is, a mid-peak in richness versus a low-elevation plateau in abundance, perhaps due to sampling of more sites across a larger geographical region. In contrast, a mid-peak was not found in our study when elevational variation within locations was ignored, for both richness and abundance (Figure S6). Taken together, this implies that future studies need to account for fine-scale variability in topography and litter depth by conducting sufficient replication within each location to quantify this heterogeneity, or to sample more locations.

Previous work shows that leaf litter depth or mass positively correlates with abundance and species diversity in rainforest ants (Grimbacher et al., 2018; Jacquemin et al., 2016). This relationship can be explained by the variable amount of leaf litter available on

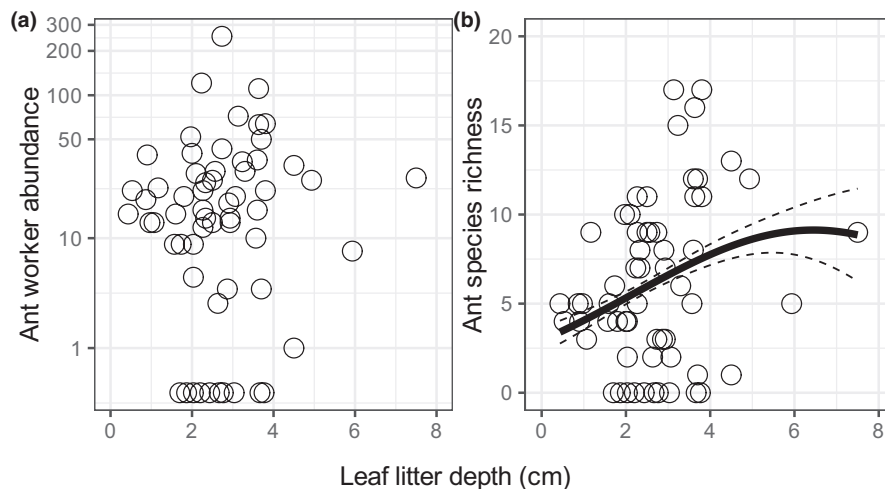


FIGURE 3 Effect of leaf litter depth on ant worker abundance (a) and species richness (b) across the 60 sampled sites. Line in (b) is fitted according to GLM prediction with standard errors as dashed lines (i.e., see Table S4 and Results for model details). Note the top 20 sites without ants (>2,746 m a.s.l.) are excluded and the log-scale plotting is used in (a)

the forest floor, where areas with greater litter depths support more individuals and species, since they provide more resources such as nesting sites and prey. These areas also have more variable humidity and microclimate, hence potentially providing niches for a greater number of ant species (Mezger & Pfeiffer, 2010). We found support for this correlation at lower elevations, where there was a positive relationship between litter depth and ant species richness. However, at higher elevations, above ~700 m a.s.l., this pattern reversed. We speculate that the change in ant richness-leaf litter relationship is driven by humidity and temperature. The higher elevations of Mt. Wilhelm experience more frequent rains than the lowlands (Leponce et al., 2016; Sam et al., 2019). Nests of ants in leaf litter and soil in mid and high elevations might be limited to dry conditions, while deeper leaf litter could be too cold and humid for ants. This may not be the case in lower elevations, where the leaf litter layer could protect ants from climatic extremes (Scheffers et al., 2014), and ant species richness may be limited only by habitat complexity, in this case leaf litter depth. Interestingly, the interaction effects between leaf litter depth and elevation on the ant richness, coupled with the changes in leaf litter with elevation, can explain the mid-elevation peak that we observed at 800 m a. s. l. This appears to be the point at which it is not so cold that large volumes of leaf litter are detrimental, but also where higher volumes of leaf litter are still beneficial. Although we did not measure humidity and temperature gradients in the leaf litter layer at our sites, previous work shows the importance of temperature gradients within forest vegetation from leaf litter up to the canopies in driving species distributions via thermal limitations (Kaspari et al., 2015; Scheffers et al., 2014). Such stratified temperature differences are likely to vary even more at higher elevations due to much colder litter but still relatively warm canopy (Scheffers et al., 2013).

The consistently negative effect of leaf litter depth on ant abundance across elevations is more difficult to explain. Some studies did find insignificant or rather weak effects of leaf litter depth on tropical ant abundances (Donoso et al., 2010; Nakamura

et al., 2009), so the positive effects on communities observed elsewhere (Grimbacher et al., 2018; Jacquemin et al., 2016) may not always occur or may vary between geographical regions or spatial scales. One plausible explanation of this unexpected pattern is that deeper litter may limit larger colonies across all elevations in our region and instead favor smaller colonies, due to more varying microclimate and higher humidity. One possible mechanism for this is if smaller colonies are more mobile, and more able to fit into small local areas of microclimate, and hence are more able to take advantage of the broader range of microclimates present in areas with deeper litter. Indeed, seasonal and vertical shifts in the composition and abundance of tropical ground-dwelling ant communities suggest a high mobility of colonies in the litter (Jacquemin et al., 2016).

The ant abundance and richness patterns that we observed with elevation may also be related to factors other than temperature and leaf litter availability, such as net primary productivity or food resources (Longino & Colwell, 2011; Peters et al., 2016; Sanders et al., 2007). The patterns could also be caused by mid-domain effects, with greatest overlap between low and high elevation species occurring at mid-elevations (Colwell et al., 2016). Niche conservatism and interglacial climate change could also potentially explain these patterns (Bush, 2002; Longino & Branstetter, 2019). The higher richness at mid-elevations may also be caused by decreased interspecific competition in comparison with the lowlands. At our study sites, we documented decreases in colony sizes and lower occurrence of behaviorally super-dominant ant species with increasing elevation as a likely driver of a mid-elevational peak in nest and species densities in arboreal ant communities (Plowman et al., 2020). Such changes in nest sizes and aggression between species with elevation are perhaps less likely to occur at the ground level than in tree canopies, due to the higher nesting site limitation in the latter habitat (Mottl et al., 2020; Philpott & Foster, 2005). However, shifts in competition may still contribute to the overall patterns in abundance and richness of ground-dwelling ants that we observed.

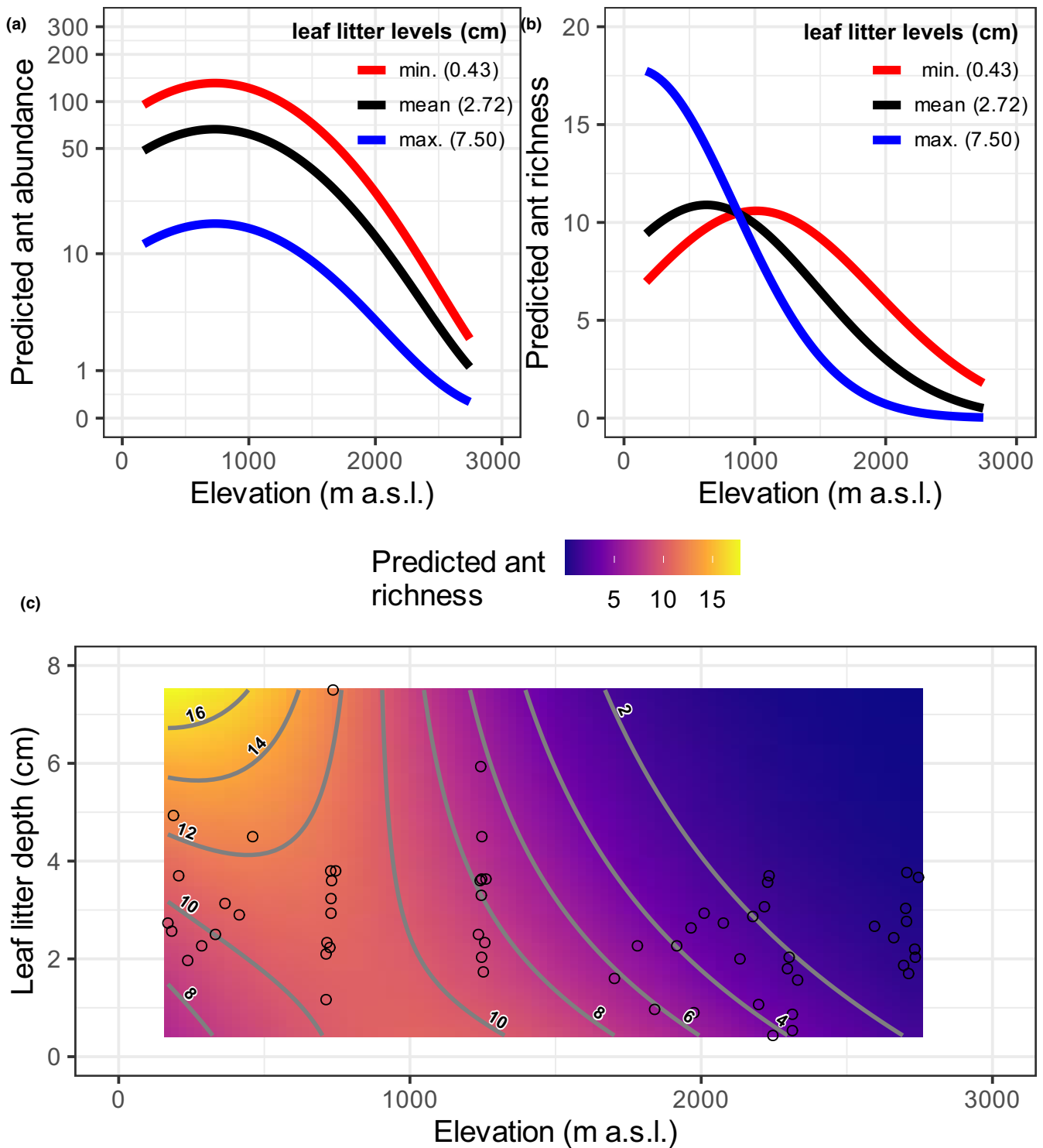


FIGURE 4 Cross-sectional plots of predicted relationships with elevation for (a) ant abundance and (b) species richness at three constant levels of leaf litter depth (0.43, 2.72, and 7.50 cm). There was a significant effect of both elevation and leaf litter depth on both ant abundance and species richness. However, when the two variables were included in the same model, their interaction had a significant effect only on species richness (b) (Table 1 and Table S4). (c) A two-dimensional contour plot for visualization of the relationship in panel (b) using a heat map and the GLM predictions of changes of ant species richness across different elevations and leaf litter depths. Black circles denote observed values of leaf litter depth/elevation at the sampled sites ($n = 60$, the elevation gradient limited up to 2,746 m a.s.l., see Methods for details). Legend abbreviations: min. = minimum, mean and max. = maximum observed values for leaf litter depth. Note the log-scale plotting is used in (a) for clarity as there are outliers

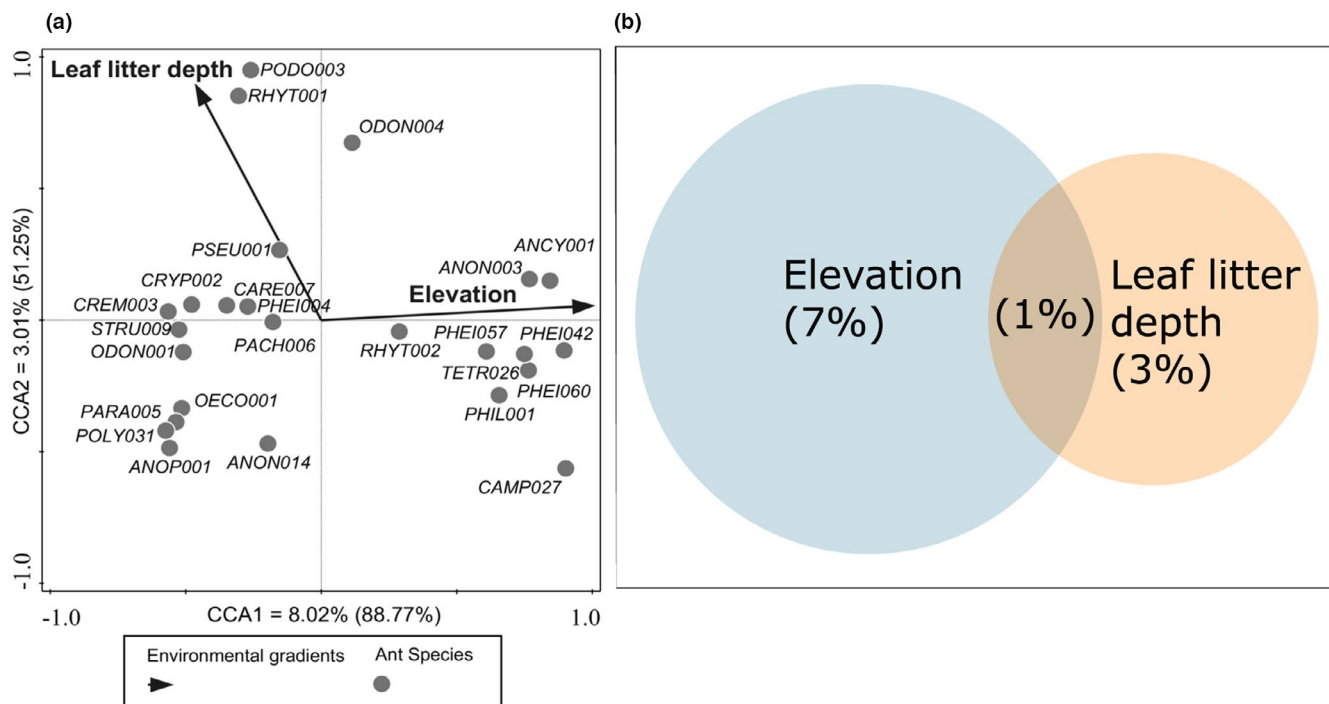


FIGURE 5 Variation in ant community composition explained by elevation and leaf litter depth in multivariate canonical correspondence analysis (CCA). (a) Ordination plot of the first two canonical axes. (b) Venn diagram showing the percentage of the variability explained by each of the two predictors independently and by their overlap. Only 25 species that were best fitting to the ordination gradient are plotted for clarity (see Table S1 for the full species names associated with all species codes and their abundances)

Unsurprisingly, there was a stronger effect of elevation than leaf litter depth on ant species composition. Ant communities exhibit rapid species turnover with elevation in the tropics, with different ant species usually dominating each elevational zone (Bishop et al., 2015; Brühl et al., 1999). This pattern is also seen in many other animal and plant taxa (Colwell et al., 2016). The possible drivers of this turnover include rainfall, humidity, food resources, vegetation structure, and dispersal barriers (Peters et al., 2014, 2016; Rahbek et al., 2019). In particular, habitat filtering may contribute to discrete boundaries between species' ranges, as the distinctive different vegetation types on Mt. Wilhelm (Leponce et al., 2016) may provide varying microhabitat complexity and thus determine the composition of ground-dwelling ant assemblages. Interestingly, we found significant effects of leaf litter depth on ant species composition that were independent of elevation effects, despite decreasing leaf litter depth with elevation. However, individual ant species were not highly specialized to different leaf litter depths. Most of the common species did not show a preference, suggesting low direct effects of leaf litter depth on the overall species composition, with the explained variability driven rather by rare species.

In summary, our study demonstrates significant changes in ant abundance, species richness and composition with elevation and leaf litter depth. We conclude that drivers of ant species diversity interact in complicated ways, with communities responding to leaf litter levels differently across elevations. Interestingly, our results predict that mountains with deep leaf litter in the lowlands

should show monotonic decreases in ant species richness with elevation, while those with shallow leaf litter in the lowlands should show mid-elevation peaks in species richness. This may explain existing observations of ant species richness in relation to leaf litter level with elevation from some other mountain ranges (Brühl et al., 1999; Marathe et al., 2020; Olson, 1994), but not in others (Sabu et al., 2008). Leaf litter depth as a driver of these patterns deserves further investigation across elevational gradients from multiple geographic areas. The complicated relationship between leaf litter depth, elevation, and invertebrate communities calls for experimental leaf litter removal and addition in order to understand the role of these factors in shaping communities on tropical mountains.

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AUTHOR CONTRIBUTIONS

JM, TMF, and VN designed the field survey; JM and TMF performed the survey and collected the data; JM and PK identified the ant species, assembled the data, and conceived the analyses; JM wrote the R codes and analyzed the data; JM and PK wrote the first draft. All authors contributed significantly to the ideas and manuscript revisions. All authors declare they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.5x69p8d1w> (Klimes et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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