

Experiments with artificial nests provide evidence for ant community stratification and nest site limitation in a tropical forest



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Abstract

Ants are dominant in tropical forests and many species nest in hollow cavities. The manner in which species are vertically stratified in these complex habitats is not known, with lack of nest sites being proposed to limit ant populations. Here, we assess ant community stratification and nest site limitation in a lowland rainforest in New Guinea using experimental addition of artificial bamboo nests of two cavity sizes (small: ~12 mm large: ~32 mm diameter) placed at ground level, in the understorey, and in the canopy. We also conducted a pilot experiment to test the utility of nest translocation. Nests were checked for occupancy after 10 weeks and half of the occupied nests were then translocated between forest plots, while keeping same vertical position. Occupancy of small nests was much higher in the understorey and canopy than at ground level (~75% vs. ~25%). Translocation was successful, as a majority of nests was inhabited by the same species before and after translocation and there was no impact of translocation to a different plot compared to the control, except for a reduction in colony size at ground level. Our experiment demonstrates a vertical stratification in community composition of ants nesting in hollow dead cavities and shows that these ants are more nest site limited in the higher strata than at ground level. Use of small artificial cavities has great potential for future experimental studies, especially for those focused on arboreal ants, as occupancy is high and translocation does not negatively affect their colony size.

Abstract in Tok Pisin is available with online material.

KEYWORDS

bamboo, canopy, community ecology, forest strata, Formicidae, nest translocation, Papua New Guinea

1 | INTRODUCTION

Primary tropical forests host the largest species diversity in the world, especially in terms of the number of vascular plants and insects (Mittermeier et al., 2003; Swartzendruber, Beehler & Alcorn, 1993). These forests are able to support such high diversity in part through their complex three-dimensional structure (Yusah & Foster,

2016). As a result of this, many groups of animals and plants are vertically stratified in tropical forest canopies (Bruhl, Gunsalam & Linsenmair, 1998; Dial, Ellwood, Turner & Foster, 2006; Fayle, Chung, Dumbrell, Eggleton & Foster, 2009). However, due to challenges in accessing the canopy, the degree of vertical stratification displayed by most groups remains poorly known, in particular for arthropods.

Ants are ecologically important, species-rich, highly abundant arthropods in tropical forests (Floren & Linsenmair, 1997; Hammond, 1992; Holldobler & Wilson, 1990). Ant colonies either inhabit pre-existing nest structures or construct their own, in order to defend the nest and maintain a territory (Holldobler, 1983; Holldobler & Lumsden, 1980). The most common types of ant nesting microhabitats are soil, dead wood, leaf litter, hollow and living twigs (Holldobler & Wilson, 1990; Lach, Parr & Abbott, 2010). Nesting in hollow cavities is one of the most common nesting strategies in ants worldwide (Carroll, 1979; Klimes, 2017). Twig nesting is present within all forest strata with colonies occupying either dead twigs on the ground (Armbrecht, Perfecto & Vandermeer, 2004; Sagata, Mack, Wright & Lester, 2010) or both living and dead hollow twigs in plants (Bronstein, 1998; Klimes, 2017; Philpott & Foster, 2005).

A number of different factors affect the distribution of ant species in hollow cavities. Height in the canopy is expected to be important, since ant communities are highly vertically stratified in tropical forest (Bruhl et al., 1998; Ryder Wilkie, Mertl & Traniello, 2010). Although this stratification has not been explored specifically for cavity-nesting ant communities across different tropical forest strata (Dial et al., 2006; Ryder Wilkie et al., 2010), some twig-nesting species in canopies prefer not only different type of twigs but different vertical heights, for example, *Colobopsis* and *Camponotus* species in New Guinea (Klimes & McArthur, 2014), and ants living naturally in bamboos in Brazilian savannas (Arruda et al., 2016). Furthermore, different cavity attributes can affect inhabitation by ants: Volume of nest cavity affects species composition and species richness in natural dead twigs on the ground (Byrne, 1994) and in bamboo stems (Arruda et al., 2016), while cavity entrance size is known to affect species occupancy in artificial bamboo nests on trees (Jimenez-Soto & Philpott, 2015; Powell, 2009; Powell, Costa, Lopes & Vasconcelos, 2011). Ants nesting in living plant tissues are usually involved in specialized interactions at ant genus or species level in myrmecophytes, sometimes utilizing the special cavities (domatia) offered by the plants, while those in dead twigs tend to host a wider range of different ant taxa, which are often less specialized to this microhabitat (Klimes, 2017). However, in some plant types, such as bamboos, certain ant species show a preference toward dead or live stems (Arruda et al., 2016; Davidson, Arias & Mann, 2006).

Because of the large populations and diversity of ant species in the tropics, ants (including those nesting in cavities) often compete for space and feeding resources (Bluthgen et al., 2000; Holldobler & Lumsden, 1980; Stanton, Palmer & Young, 2002). There is thus a high demand for nesting sites, and their availability is postulated to be a limiting factor for ant communities (Armbrecht, Perfecto & Silverman, 2006; Powell, 2009). Although this nest site limitation hypothesis has been supported by experimental studies in plantation habitats (Jimenez-Soto & Philpott, 2015; Philpott & Foster, 2005), it has not been tested in primary tropical forests in more than a single stratum (Byrne, 1994; Sagata et al., 2010). Most studies of nest site limitation have focused on arboreal species but this limitation is likely to be a more general phenomenon in ant communities: It has also been found in ant ground fauna in the temperate zone in natural

habitat (Foitzik & Heinze, 1998; Herbers, 1986) and in urban ecosystems (Friedrich & Philpott, 2009). However, to our knowledge, no study has compared the occupancy of cavity-nesting ant communities among forest strata at the same site.

Although observational studies are valuable for exploring the factors controlling ant communities, further insights into complex tropical systems require manipulative experiments. Such experiments can distinguish if observed patterns are driven only by environmental variables (habitat filtering) or species interactions (competition, etc.). However, because ants are colonial, it is necessary to carry out manipulations on whole colonies, rather than on individuals. Experiments have already been successfully conducted by adding ant colonies into the ecosystem (Fowler, 1993) or translocating colonies of single species using semi-artificial nests (Peng, Nielsen, Offenberg & Birkmose, 2013; Riginos et al., 2015). At the level of whole ant communities, artificial bamboo nests have been used successfully for experimentally testing the effect of nest additions to the ecosystem (Davidson et al., 2006; Philpott & Foster, 2005), entrance-nest sizes (Arruda et al., 2016; Fagundes, Terra, Ribeiro & Majer, 2010; Jimenez-Soto & Philpott, 2015; Powell, 2009), vegetation connectance (Powell et al., 2011), and competitive interactions (Mathis, Philpott & Ramirez, 2016). The method is popular due to low cost, ease of manipulation of nests, and the ability to standardize in terms of bamboo species and cavity size. This is important as wood species diversity affects communities of twig-nesting ants (Armbrecht et al., 2004). However, whether the artificial nests are suitable for translocating colonies has only been investigated in agricultural habitats for a certain ant species (Wielgoss et al., 2014), while the utility of bamboo translocation for ants remains unknown in natural habitats and at the level of whole communities. Despite increasing use of the artificial nests for ants in situ, it is not clear if nests can survive when translocated in natural systems, hence allowing the use of this method for community manipulation. In the tropical forests, where different vegetation successional stages and strata affect ant species richness and composition, and with variable level of ant dominance and co-occurrence patterns (Bluthgen & Stork, 2007; Klimes, Fibich, Idigel & Rimandai, 2015; Ribeiro, Espirito Santo, Delabie & Majer, 2013), translocation could be used to manipulate communities to assess the relative contribution of abiotic and biotic drivers on cavity-dwelling communities.

We conducted a study in a lowland primary forest in Papua New Guinea using artificial bamboo nests to answer the questions: (a) How does occupancy differ between forest strata and cavity sizes of a bamboo nest? We predict that nest site limitation will be lower at ground level and that artificial nests there will have lower occupancy, regardless of their size. This is because the ground surface has a much higher natural cavity-nest density compared to the understorey and canopy in New Guinean lowland forest (~12 500 nests in dead twigs and branches on the ground compared to ~200 such nests in trees per ha, see Figure 1 and Appendix S1). (b) How does ant species richness and species composition differ between forest strata, and between different sizes of a bamboo nest? We predict differences in species composition between ground and canopy (Lasmar et al.,

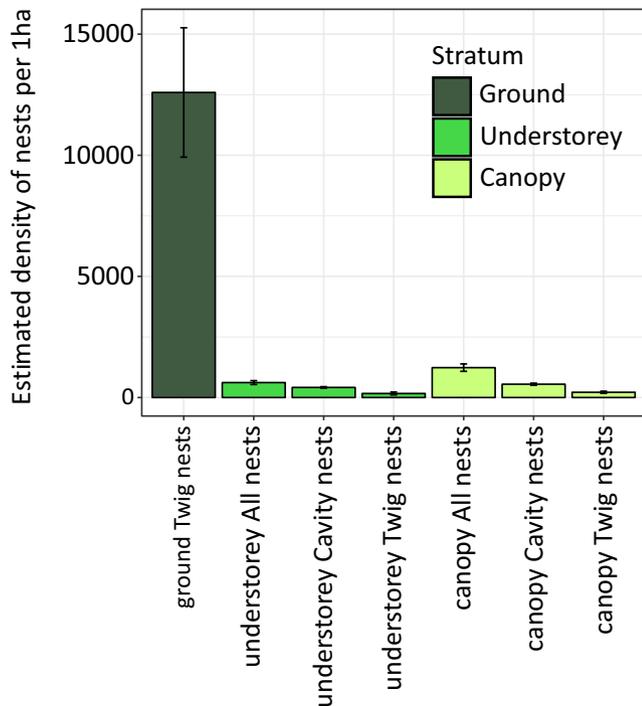


FIGURE 1 Estimation of natural nest densities of ants in a hectare of lowland forest in New Guinea (mean \pm SE). Understorey trees are defined as the stems with DBH \leq 10 cm. Twig nests are those in dead/rotten twigs/branches. Cavity nests also include those in live twigs/branches and whole trunk cavities. For detailed information on used datasets and calculation, see Appendix S1 and Klimes (2017)

2017; Ryder Wilkie et al., 2010), and that different species should be attracted to nests of different cavity sizes (Jimenez-Soto & Philpott, 2015; Novais, Darocha, Calderón-Cortés & Quesada, 2017; Powell et al., 2011) (c) Does translocation of the artificial nests to a different location affect the survival or size of colonies? We predict that nest translocation should have a negative impact (reduction in survival or colony size) due to disturbance of the colony regardless of where the nest is moved. Also, we predict that nests translocated to different forest plot should experience greater negative impacts than those that returned to the same plot, as translocation over longer distances is more likely to disrupt micro-environments, foraging trails, competition and access to currently utilized feeding resources (Bluthgen et al., 2000; Holldobler & Lumsden, 1980).

2 | METHODS

2.1 | Ant survey

Fieldwork was conducted in lowland primary forest in Baitabag conservation area, Madang Province, Papua New Guinea (5°08'30.0"S, 145°46'30.5"E, elevation 50 m a.s.l.) between July and October 2016. We set up four plots of 25 m \times 25 m (A, B, C, D) ~100 m apart. Initially, we surveyed the ant activity using baits made of a mixture of canned tuna in oil and honey (5:1 ratio). We placed one spoon of the mixture (approximately 5 g) on a paper towel (7 cm \times 7 cm). We

divided each plot into 25 subplots of 5 m \times 5 m. One bait was placed onto the ground in the middle of each subplot, and one was placed onto the nearest understorey vegetation at 2 m height (25 baits on the ground and 25 in the understorey per plot). After three hours, we estimated the abundance of each ant species on each bait (number of individuals: 1–5; 6–10; 11–20; 21–30; 31–50; 51–100; 101–150; 151–250) and collected several individuals into 98% ethanol for later identification. All ant species were determined using keys (Andersen, 2000; Bolton, 1995), online picture databases (antweb.org, newguineants.org), and morphological characters.

2.2 | Artificial nest design and placement

We created 300 artificial nests of two cavity sizes (150 small and 150 large) from a local bamboo species. Each nest was 15 cm long and was sealed at one end by a naturally occurring node and open at the other. Large nests had a mean inner diameter of 32.4 mm (*Bambusa atra*, span: 24–34 mm), and small nests had a mean inner diameter of 12.5 mm (*Bambusa textilis* var. *gracilis*, span: 8–19 mm). Our aim was to choose stems of similar diameter as possible within each category, and hence, the variation of cavity diameter within the two categories was small (Figure S1). We chose common local softwood for wooden plugs to seal the open hole of each nest. The nest design was adapted from (Jimenez-Soto & Philpott, 2015; Powell et al., 2011), but with increased length (15 cm instead of 10 cm) and with two drilled holes (instead of only one hole). One hole was 2 mm diameter in the middle of the bamboo, and one was 6 mm diameter near to the node (Figure S2). Previous studies showed that entrance size affects ant species preference for the nests (Powell et al., 2011) and that length and diameter of cavity affects the ants nesting in bamboos (Arruda et al., 2016; Fagundes et al., 2010). Our modification (two cavity sizes, two entrance sizes, longer bamboo) was thus intended to increase the chance of occupancy of our artificial nests by a wider range of species.

At the start of July 2016, in each plot, we placed nests into three different strata: the canopy, understorey, and ground (Figure S3). Two plots were used for large nests (A and B plots), and two plots for small nests (C and D plots). Our interest was to test for general suitability of the methods with bamboos of different cavity size types for the occupancy and translocation experiments among plots, rather than to test for local species preference for each cavity size, where a paired size placement would be more suitable. Twenty-five nests of a given cavity size were placed into each stratum (25 artificial nests added per plot and per stratum, 75 per plot in total). We used a slingshot to install ropes into the canopy of the highest trees in each plot (regardless of the subplots) and measured vertical height of each nest (mean \pm SD 16.4 \pm 4.5 m). Nests were attached to ropes with cable ties and placed onto branches by maneuvering and tying off the rope at ground level. We confirmed that the nests were touching branches with binoculars. In the understorey, we chose one small tree in each 5 m \times 5 m subplots that had been used for baiting and attached the nest with cable ties at a height of 4–5 m (we did not measure the exact height for these nests and 5 m was used in

all analysis). On the ground, we placed nests under each previously selected understorey tree. Tree species identities were not recorded in this study. However, detailed data from a similar forest as at our site showed very low effect of trees species on the ant communities in New Guinea, in particular on those nesting in dead branches (Klimes, 2017).

2.3 | Nest translocation experiments

Ten weeks after initial placement, we checked nests for ant occupancy and sampled 1–2 individuals into 98% ethanol from occupied nests for identification. A hand lens (30×) was used in the field to identify the morphospecies and IDs were later confirmed to species level in the laboratory (see below). Sampling and manipulation were conducted carefully to reduce disturbance. Nests were either gently tapped to provoke ant workers to emerge, or the plug was briefly removed. Unoccupied nests and nests occupied by other insects were removed. Those occupied by ants were placed then into plastic ziplock bags and kept out of direct sunlight for ~1 hr. We then randomly assigned each nest to translocation or control, with half of the nests occupied by each morphospecies being placed back into their original plots (same stratum and same plot, treatment “stay”), and the other half being placed into the same stratum but in different plots (A↔B and C↔D, treatment “move”). In cases where there were odd colony abundances for a morphospecies, the remaining single nest was randomly assigned a treatment.

We left the translocated and control nests exposed for four more weeks and then collected all nests into plastic ziplock bags and killed the ant colonies by placing the bags in a freezer (approximately –10°C). Each nest was then dissected, all material was stored in 98% ethanol, and numbers of queens and workers and the presence of brood were recorded. Field-based species-level identifications were verified in the laboratory using existing collections of PK from the region (Klimes et al., 2015) and other identification resources (see above). Samples from this study are stored at the Institute of Entomology, CAS, Czech Republic. We scored nests as (a) died, (b) being occupied by the same species as before being moved and (c) being occupied by a different ant species at the end of the experiment. For part of the analysis, we also distinguished between “active” nests (nests with brood and/or queen) and “non-active” nests (nests with only workers).

2.4 | Data analysis

Analyses were conducted in R 3.5.2 (R Core Team 2016) using various packages (see below) and CANOCO 5.04 (Braak & Smilauer, 2012).

We used multivariate analysis to test for differences between our plots and between the two strata (ground and understorey) in species composition of ants sampled using tuna baits. Data were entered as a matrix of individual baits by ant species with entries being the estimated abundance of that species on that bait. Only species that occurred on more than two baits were included in analysis. We

performed Canonical Correspondence Analysis (CCA) with forward selection of explanatory variables (stratum (two levels) and plot identity (four levels)) to find variables best explaining the species composition (*p* values corrected using “False discovery rate” to reduce type I errors (Braak & Smilauer, 2012), 999 randomizations). We then also performed two CCAs for each stratum separately, with only the plot identity as the explanatory variable.

To explore whether nest cavity size and stratum affected occupancy of the nest we created Generalized Linear Mixed Models using Template Model Builder (glmmTMB) (Brooks et al., 2017) with proportion of occupied nests in each plot at the end of the first census (i.e., after 10 weeks) as the dependent variable with beta-regression error distribution. We used nest cavity size (large/small) and position in strata (canopy/understorey/ground) as fixed categorical factors and plot (A/B/C/D) as a random factor. We built the best model, starting from a null model (~1) using forward selection.

We used a Cox proportional hazards regression model (Therneau & Grambsch, 2000) to test for differences in nest survival rates between treatments. Nest cavity size (large/small) and plot (A/B/C/D) were used as random variables. We considered all nests together (i.e., we did not include nest cavity size as a factor), because low occupancy of large nests (see Results 2.1) did not allow the testing of effects of nest size separately. We conducted three separate analyses. First, we counted a nest as having survived if it was occupied by the same species before translocation and at the end of the experiment. We tested for effects on survival of translocation treatment (stay/move), stratum (canopy/understorey/ground) and their interaction. Second, we repeated the same analysis but counted a nest as having survived only if it was occupied with same species and had a queen and/or brood (i.e., active nest) at the end of the experiment. Third, we calculated survival rates corrected for abandoned (dead) nests that were potentially re-occupied by the same species using a conservative probability model that assumes a linear occupation in time (see Appendix S1).

We tested if translocation and forest stratum affected colony size of nests occupied at the end of the experiment for all three above situations. We calculated colony size as the natural logarithm of the number of all adult individuals in the nest and created a linear mixed-effects model (LMM) (Bates, Mächler, Bolker & Walker, 2014) with colony size as the dependent variable. Nest cavity size (large/small), ant species identity and plot (A/B/C/D) were set as random effects. We tested if translocation treatment (stay/move) and stratum (canopy/understorey/ground) affected colony size. Next, we tested if there was a significant difference in the number of nests with queens between translocation treatments (stay/move) using a Generalized Linear Model (GLM) (Dobson & Barnett, 2008) fitted with Poisson error distribution.

Next, our aim was to test how different properties of nesting microhabitats affect species richness and composition found in the artificial nests. Species data per plot, both from before translocation and from the end of the experiment, were pooled for analyses. To assess differences between strata and nest cavity size in terms of species richness, we calculated number of species in each

stratum per plot and created a Generalized Linear Mixed-Effects Models (glmer) (Bates et al., 2014) with species richness as dependent variable with Poisson error distribution, nest cavity size (large/small) and stratum (canopy, understorey, ground) as fixed categorical factors and plot (A/B/C/D) as a random factor. We also included an interaction between these two predictors. We used multivariate analysis to test which properties of artificial nests affected the species composition of resident ants. We selected two predictor variables: a) size of nesting cavity (in mm) and b) height of nest (0 m for ground, 5 m for understorey and exact measurements for canopy). Data were entered as a binary matrix of nests by ant species, and plot identity was set as a random factor. Because we had information about species nesting in each bamboo both before translocation and at the end of the experiment, we pooled data from both censuses and used presence-absence scores for each nest for each ant species. Only species that occurred in more than one nest were included in analysis. First, we performed CCA with the variables tested by forward selection (999 randomizations, “False discovery rate” correction of p values). The efficiency of each axis was calculated as the ratio of variability explained by constrained and unconstrained analyses. Second, we calculated species response curves for those variables identified as being significant predictors in the CCA of ant community composition. Separate GLM models (null, linear, second level polynomial) were calculated for each ant species (present in more than one nest) and the significance of their relationships with predictor variables was tested using F tests. For each species, we selected the best-fitting significant models based on their deviance.

3 | RESULTS

3.1 | Ant survey

We found 25 species of ants in 15 genera across all sampling methods combined (tuna baiting and artificial nests). For tuna-baiting community, composition differed significantly between forest strata (pseudo- $F = 8.9$, $p < 0.01$, Table S1, Figure S4). However, there were

no differences between plots for the ground communities (pseudo- $F = 1.5$, $p = 0.070$), or those collected on vegetation (pseudo- $F = 1.1$, $p = 0.337$; note that the canopy was not sampled using tuna baits). Therefore, we assume that the different plots have a homogenous species pool.

3.2 | Artificial nest occupancy

After 10 weeks, 120 out of 300 nests were occupied by ants (27 large and 93 small) in three different strata (46 in the canopy, 47 in the understorey and 27 on the ground, Figure 2). A small number of nests in both censuses were occupied by termites that were probably attracted by the wooden plugs (11 nests). We did not observe any bees or wasps in our nests. Seven (2.3%) nests were damaged during the exposure and were excluded from the analysis. Across the 293 undamaged artificial nests exposed, ant occupancy per plot varied between nest cavity size and strata, with a maximum of 88% occupancy for small nests in the understorey and a minimum of 12% in large nests in the understorey after 10 weeks. We found that the best model included nest cavity size, stratum and their interaction (deviance test, $p < 0.05$, Table S2), with large nests across all strata and small nests at ground level having lower occupancy (mean 22%) when compared to small nests in the understorey and canopy (mean 79%) (Figure 2).

3.3 | Survival rate

In total, from the 120 nests occupied after 10 weeks, 81 nests (67.5%) were also occupied at the end of translocation experiment after a further four weeks. Of those, 40 (49.4%) had queens and/or brood. There was no significant difference in colony survival between nests that were moved to a different plot and nests returned to same plot (Score (logrank) test, Robust = 0.05, $df = 1$, $p = 0.828$; Figure 3). There was also no significant difference in survival between strata (Score (logrank) test, Robust = 3.03, $df = 2$, $p = 0.220$). Counting only nests with queen and/or brood as survived did not change the results (Table S3). Survival rates did not significantly change between the treatments when corrected for the proportion

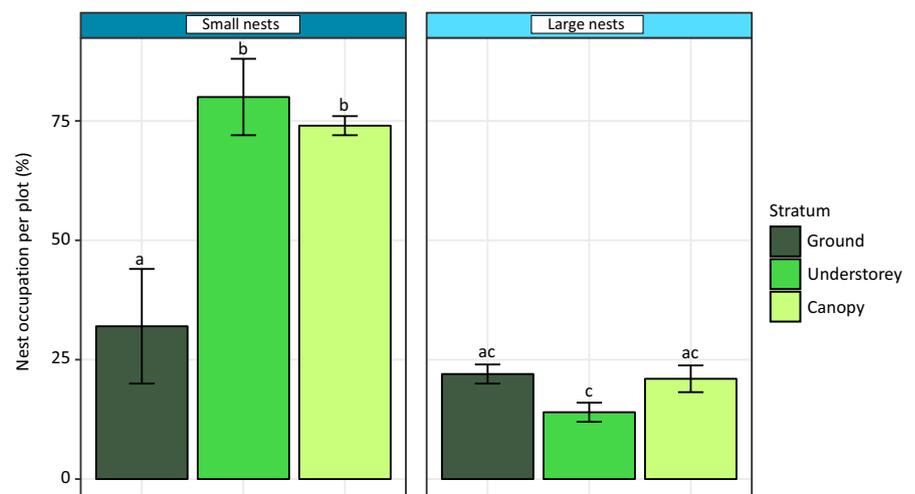


FIGURE 2 Mean occupancy of artificial bamboo nests by ants in each stratum after ten weeks of exposure in the field. Error bars show standard errors. Letters show significant differences between nest cavity size types and strata (glmmTMB, $p < 0.05$). The best model was one with both factors and their interaction (see Results 3.2 and Table S2 for details)

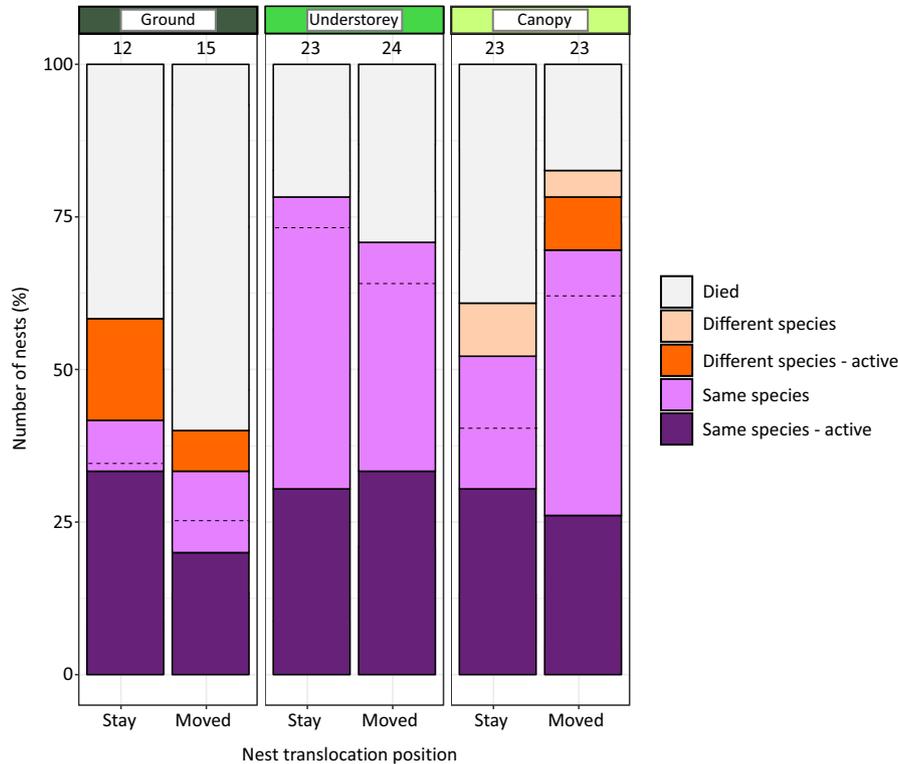


FIGURE 3 Survival rates of ant colonies in artificial nests. Approximately half of the occupied nests in each plot and stratum after ten weeks were moved into a different plot and half remained in the same plot (numbers above the bars refer to the numbers of nests). Nests were checked again after a further four weeks. The results from small and large nests are combined and each nest is scored as follows: died (no ants were found in the nest), different species (different species of ant were found before and after translocation), same species (no change in species identity), different species—active (different species with queen and/or brood presence in the nest), same species—active (same species with queen and/or brood). There was no significant difference in colony survival between moved nests and nests returned to the same plot, and also no significant difference between strata (see Results 3.3 and Table S3 for more details). The dotted horizontal line in each column denotes the estimated proportion of nests that survived after correction for the nests that potentially died and were re-occupied by the same species, based on the observed natural nest occupancies prior to translocation (see Appendix S1 for the calculation). The difference between this line and the top of the “same species” blocks represents the estimated bias

of nests, which potentially did not survive and were then re-occupied by the same species (Figure 3 and Figure S5, Table S4). We also did not find a significant difference in the number of nests with queens between translocated and control treatments (test of deviance; $df = 2, 9$; $p = 0.509$).

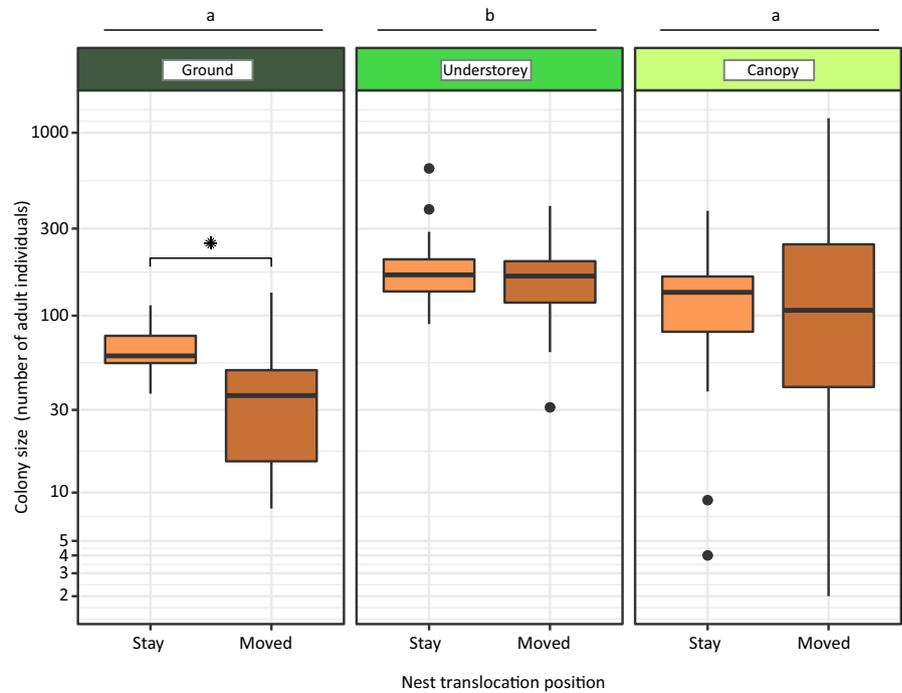
3.4 | Colony size

The number of adults in the 81 nests at the end of the experiment ranged from two to 1200 individuals (mean 157.2). There was a significant difference in colony size between strata (Chisq = 14.56; $df = 2$; $p < 0.01$; Table S5), with understorey nests having the largest numbers of adults (Figure 4). There was not a significant effect of translocation when data from different strata were combined (Chisq = 1.85; $df = 1$; $p = 0.178$). However, colony sizes were significantly smaller for translocated nests placed at ground level compared with non-translocated nests when testing each stratum separately (Chisq = 4.79, $df = 1$; $p < 0.05$).

3.5 | Species richness and composition in artificial nests

In total, 14 species were found to nest in the artificial bamboo nests (Figure 5). The number of species per plot in each stratum ranged from one to four. However, there were no significant differences in species richness between nest cavity sizes (test of deviance; $p = 0.705$) or strata (test of deviance; $p = 0.509$) (Table S6, Figure S6). Forest stratum significantly affected ant species composition (pseudo- $F = 14.1$, $p(\text{adj}) < 0.01$, Figure 5c, Table S7) and explained 11.3% of variability (10.5% adjusted), while the cavity diameter did not influence species composition. Four species showed significant responses to nest stratum (Table S8). A single species, *Colobopsis vitrea*, dominated both understorey and canopy, but at ground level *Nylanderia aff. vaga* was the most common (COLO 001 and NYLA 005 sp. codes in Figure 5, respectively). There was no species overlap between the ground and either of the two arboreal strata, except one understorey nest of *N. aff. vaga*.

FIGURE 4 Differences in colony sizes between translocation treatments in different strata at the end of the experiment. Half of the occupied nests in each plot after ten weeks were moved into a different plot and half stayed in their original plot for four weeks more (see Methods2 for details). Significant differences between strata are indicated by letters above the panels, and differences within each stratum by stars above the box plots. Central bold lines indicate medians, boxes the 1st and 3rd quartiles of the data, and whiskers 1.5 times the interquartile range. Outliers beyond the range of the whiskers are plotted as circular points



4 | DISCUSSION

We predicted that nest site limitation, measured by the occupancy of artificial nests, would be lower on the ground level. Our results do confirm this for small nests, with the canopy and understorey having three times higher occupancy than the ground level. We speculate that the higher occupancy of smaller cavities we observed could be due to naturally smaller wood diameter used by most ants in the tropical forests (Sagata et al., 2010). Smaller nests exposed in trees are therefore suggested for future experiments, since this would allow greater numbers of colonies to be sampled. We confirmed our prediction of strong stratification patterns of tropical ants both in nests and on baits. Similar patterns have been observed in another lowland forest in Papua New Guinea (Klimes, Janda, Ibalim, Kua & Novotny, 2011) and elsewhere (Ryder Wilkie et al., 2010). Surprisingly, we did not find an effect of nest cavity size on species composition, in contrast to previous studies (Bruhl, Eltz & Linsenmair, 2003; Novais et al., 2017; Powell, 2009; Powell et al., 2011). Although the only variable that affected species composition was vertical nest height, there was a similar occupancy and species composition when only understorey and canopy were compared. This rather homogenous species composition in bamboo nests in strata aboveground level is likely to be driven by the most common species, *Colobopsis vitrea*, which was found in 69% of all occupied nests. However, there was a difference in species composition between the communities found on baits and in nests, with a higher richness observed on baits. Hence, even though we did not find any preferences for nest size, the experimental community was a subset of the local community of ant species. Indeed, a full census of arboreal nests in the region found over 100 species in a 0.3 ha area (Klimes et al., 2015).

The unexpectedly high dominance of few species in the artificial nests could be driven by a preference of non-dominant opportunistically nesting species for dead hollow cavities (and bamboo nests) at our site and by the fact that these species were more abundant in the canopy. We found that *Colobopsis vitrea* (COLO 001) and *Nylanderia aff. vaga* (NYLA 005) were more common in artificial nests than at tuna baits, with the former species being also more common in our nests in the canopy. The two species are non-dominant, opportunistically nesting in many microhabitats, including dead twigs (Klimes, 2017; Klimes & McArthur, 2014). *Colobopsis vitrea* often also lives inside territories of super-colonies of *Crematogaster polita* (CREM 003: the most common species observed here at baits), and they are probably in a mutual parasitism (Klimes personal observation). This might further increase *C. vitrea* presence in the bamboos, as the aggressive *C. polita* builds natural nests from a carton, and thus rarely occupied our bamboos, although the two species tolerate each other. Further experimental studies on these two species are needed to test if the higher nest occupancy in the canopies was driven also by these interspecies interactions. Nevertheless, it is evident that even *C. vitrea* was limited by nest sites at our study area, as it nests in much lower densities in trees naturally than we observed in the artificial nests (Klimes, 2017).

Encouragingly, translocation did not affect colony survival in any stratum. However, the colony size of nests on the ground was smaller for those that had been translocated, suggesting that the microhabitat of surroundings is more important for nests on the ground. Indeed, micro-environmental characteristics such as litter amount and local temperature and humidity have been shown to drive the litter ant abundance and diversity (Delsinne, Arias-Penna & Leponce, 2013; Grimbacher et al., 2018). An alternative explanation might be increased competition of the transferred nests with

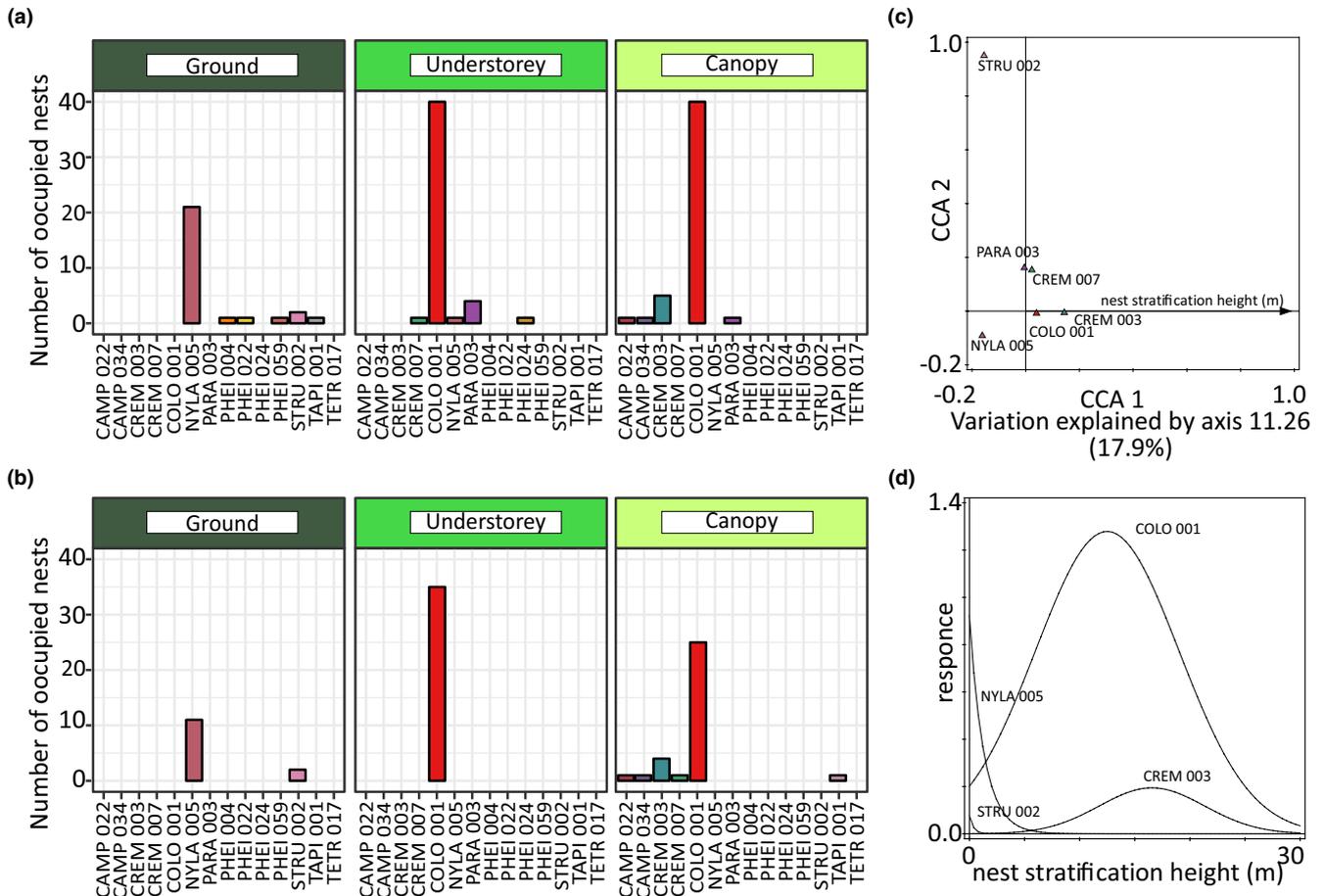


FIGURE 5 Species composition of ant colonies in artificial nests and variables influencing this composition in three different strata (ground, understory, canopy). Species are represented by codes; for full names see Table S10. (a) Species composition of nests after 10 weeks, before the translocation treatment. (b) Species composition of nests after 14 weeks, at the end of the experiment. (c) Ordination diagram of Canonical Correspondence Analysis (CCA) of variability in species community explained by the vertical height in which individual nests were placed. (d) Ant species response curves to a vertical height of artificial nest. Only species with significant responses are plotted. See Table S8 for all species responses and chosen models

natural nests on the ground. However, this is less likely given the very high natural abundance of such nests in PNG region (Figure 1) and elsewhere in tropical forests (Byrne, 1994). In contrast, canopy ants are more resistant to desiccation (Kaspary, Clay, Lucas, Yanoviak & Kay, 2015) and are more omnivorous in their diet (Davidson, Cook, Snelling & Chua, 2003), and thus might be less vulnerable to translocations. It might also be the case that more workers were left outside of nests when had been translocated on the ground, and were therefore lost to the colony.

The method of using bamboos as artificial nests for sampling whole colonies of ants is useful for two reasons: (a) Costs are low because the bamboo stem is a relatively cheap material found in most tropical regions and wooden plugs can be made locally. (b) With the exception of the nests placed in the canopy, the initial placement and collection of nests is fast with the limiting factor being exposure time (here 10 weeks prior and 4 weeks after translocation), and nests can be easily translocated and dissected. Despite the clear utility of this method, it has also some limitations. First, it can be used only for a subset of opportunistic-nesting species,

and not for live-stem or carton-nesting specialist ants (e.g., the genera *Tetraponera*, *Anonychomyrma*, *Polyrhachis* in PNG). Second, we conducted the study in a homogenous forest dominated by a supercolony of *Crematogaster polita* and we, therefore, did not observe significant differences in species composition between plots. Although this means that our plots were highly comparable with each other, patchiness of species distribution is well known in lowland tropical forests (Bluthgen & Stork, 2007; Dejean et al., 2015; Yusah, Foster, Reynolds & Fayle, 2018) and presence of different dominant species can influence the species composition (Arnan, Gaucherel & Andersen, 2011; Morrison, 1996; Room, 1971). Therefore, the occupancy may differ between forest areas at larger scales and it is not known whether our method would work successfully in areas with different species composition (e.g., outside territories of *C. polita* and *C. vitreus*). However, as the ecological niche of cavity dwelling is common around the world (Carroll, 1979; Klimes, 2017), we expect this method would work well elsewhere.

Ant colonies can be polydomous or create queen-less satellite colonies (Jimenez-Soto & Philpott, 2015) and hence measuring

survival of nest colonies is complicated. Although some studies consider occupancy of nests based on presence of a queen and/or brood (Friedrich & Philpott, 2009; Philpott & Foster, 2005; Sagata et al., 2010), the majority of studies do not give any details about colonies and consider simply nests as occupied if workers are present. Here, we show that conclusions are similar if we consider only active nests with queen or brood or all nests.

Natural turnover of ant species in cavity-nesting habitats is poorly known and varies greatly between species: some underground nests last several years (Thurber et al., 1993), while some twig-nesting species can migrate after tens of days (Byrne, 1994). Hence, it is likely that rates of colony migration varied between species within the ant community we studied. It has been demonstrated previously that re-assessment of nests after a ten-week period is long enough to observe species (and hence colony) turnover (Armbrecht et al., 2006; Philpott & Foster, 2005; Sagata et al., 2010). However, because we ran our experiment for only further four weeks following translocation, the bias of re-occupation by the same species is likely to be small in our study, despite the high dominance by a single species in each stratum. Even though we cannot directly confirm that records of the same species observed in the nest before and after translocation are the same colony, the observed survival rates are likely to be only slightly smaller if corrected for these possible new establishments (max ~11%; Figure 3). Furthermore, the result of our analysis of the difference in survival among nests translocated between and within plots does not change following this correction (see Table S4). Finally, if this bias were important, colony size would be expected to decrease (because some nests would be new), which we did not observe on vegetation. To decrease this (small) bias in future studies, we recommend checking nests multiple times both before and after translocation.

This study, for the first time, confirmed experimentally a strong stratification of communities of ants nesting in hollow twigs between the ground level and arboreal strata in a tropical rainforest and demonstrated a stronger nest site limitation in the canopy and understorey compared to the ground. We also showed the utility of the method of translocating whole ant colonies. There is great potential in experimental ecology for manipulative experiments of ant colonies between strata (and other ecological gradients). For example, shifting taxa typical for a certain environment (from disturbed forest to primary forest, or among sites of different temperature or among different species territories) could be used to test for drivers of ant distribution and community composition. All this could help to advance our understanding of complex interactions between ant species in ecosystems such as tropical forests.

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AUTHOR CONTRIBUTION

OM and PK designed the study. OM and JY performed the experiments. OM analyzed and interpreted data, and led manuscript writing. OM, JY and PK identified ant specimens. PK and TMF contributed significantly to the text, the ideas and interpretation of the results. VN provided financial resources and co-supervised the work with PK. All authors critically revised manuscript and gave final approval for publication.

DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0p32m6c> (Mottl, Yombai, Fayle, Novotný & Klimeš, 2019).

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