

The influence of nest availability on the abundance and diversity of twig-dwelling ants in a Papua New Guinea forest

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Abstract Tropical ant communities are frequently diverse, but highly patchy in nature. The availability of suitable nest sites may be a regulating force in structuring litter ant communities. Our aim was to examine ant resource utilization in naturally occurring twigs, and to modify the availability of these resources in order to quantify the influence of nest availability on ant communities in a Papua New Guinean forest. First, we compared ant communities that assemble in artificial twigs (drilled, wooden dowels), naturally occurring twigs, and the leaf litter. A total of 55 ant species were captured: 33 from the leaf litter, 29 from naturally occurring twigs, and only 12 from artificial nests. Significantly different communities formed in each of the three nest types. Second, we examined how the density of natural or artificial nest material influenced the ant abundance and species richness. Plots had between 5 and 96 potential nest sites. An average of only 11.2% of these twigs was colonized. Both species

richness and the total abundance of adult ants were significantly positively correlated with increasing naturally occurring twig density. Conversely, increasing the availability of artificial nests from 5 to 20 per plot had no significant effect on the proportion of artificial nests colonized, species richness, or the colony size. We observed that ant species richness and abundance increased with natural twig density, at least for naturally occurring communities. But why so many twigs remain vacant and available for ant colonization remains unknown. Other biotic and abiotic factors likely influence the use of nesting habitat in these ant communities.

Keywords Artificial nest · Litter ants · Nest colonization · Tropical forest · Twig-dwelling ants

Introduction

Ant diversity and abundance in tropical forests far exceed that of all other social insects (Davidson, 1997; Wilson, 1959). The densest concentrations of litter ants are found in small pieces of rotting wood, twigs, leaves, plant domatia or hollowed seeds (Kaspari, 1996a; Wilson, 1959). These materials are dynamic and usually decay faster than the life of the ant colony, thereby requiring the ants to frequently re-colonize new twigs (Byrne, 1994). The availability of suitable nest sites may therefore function as a strong regulating force in structuring litter ant communities. Previous work has found that nest site availability limits twig-dwelling ant distributions (Armbrecht et al., 2004; Foitzik and Heinze, 1998; Fonseca, 1999; Herbers, 1986; Kaspari, 1996b; Levings, 1983; Soares and Schroeder, 2001) (but see Byrne, 1994; Levings, 1983; Soares and Schroeder, 2001).

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Twig-dwelling ants in the tropics are patchy, which could also be due to an uneven distribution of nest sites (Byrne, 1994; Hölldobler and Wilson, 1990; Kaspari, 1996b; Levings, 1983; Levings and Franks, 1982; Wilson, 1958) size and diversity of twig resources (Armbrecht et al., 2004; Philpott and Foster, 2005). In Papua New Guinea (PNG), the densest concentrations of litter ants are found in rotting wood, though these communities exhibit considerable variation between localities (Wilson, 1959). Whether such differences in the ant fauna are due to the patchy distribution and density of twig nests is unclear. It is possible that twig-dwelling ants in PNG are limited by size, availability or diversity of potential twig nests as has been suggested in ant communities elsewhere (Armbrecht et al., 2004; Byrne, 1994; Foitzik and Heinze, 1998; Fonseca, 1999; Herbers, 1986; Kaspari, 1996b; Levings, 1983; Soares and Schroeder, 2001). The use of artificial nests to study twig-dwelling ants in New Guinea forest could shed light into this area because artificial nests have proven effective in studying community distribution of twig-dwelling ants in other parts of the world (Armbrecht et al., 2004; Byrne, 1994; Herbers, 1986; Kaspari, 1996b; Levings, 1983; Philpott and Foster, 2005; Soares and Schroeder, 2001).

The New Guinea ant fauna is most diverse in lowland to mid-elevation humid forests (Snelling, 1996; Ward, 2000; Wilson, 1958, 1959). However, their ecology and the role of resources shaping community structure are largely unexplored. Here, we hypothesized that the abundance and diversity of twig-dwelling ants would be positively correlated with increased nest availability. Our aim was to examine resource utilization by ants in naturally occurring twigs, and to modify the availability of these resources in an attempt to experimentally quantify the influence of nest availability on the ant community in a Papua New Guinean forest.

Methods

Study site

This study was conducted at Crater Mountain Biological Research Station (CMBRS), 10 km east of Haia village in Simbu Province, Papua New Guinea (06°43.4'S, 145°05.6'E). The study area contains pristine primary forest with patches of secondary growth, plus openings formed by landslides and frequent tree falls. Vegetation ranges from mixed evergreen hill forest to sub-montane forest (Pajmans, 1976) from 850 to 1,350 m a.s.l. Tree diversity is high with no strongly dominant canopy species, annual rainfall averages 6.4 m per year with no distinct wet or dry season, and daily temperature ranges from 15 to 28°C

(Wright et al., 1997). Fieldwork was conducted from March to September 2001.

Comparing artificial twig, natural twig, and litter ant communities

Winkler extractors were used to sample the leaf litter ant community. Four parallel 50-m-long transects at 30 m intervals were established, and leaf litter was sampled from 1 m² plots at every 5 m along each transect (for a total of 40 plots). Leaf litter from each plot was extracted through a sieve (8 × 8 mm); the fine litter was filled into mesh bags (4 × 4 mm), and the bags were placed inside Winkler extractor cloth sacks for passive extraction of arthropods (Ward, 2000). After 4–5 days, the collecting jars at the bottom of the sacks were removed, and the ants were sorted into morpho-species. Three days is a recommended time frame in which most of the species in a sample can be collected (Bestelmayer et al., 2000; Ward, 2000).

To collect naturally occurring twig-dwelling ants for comparison with the fauna from artificial twigs and leaf litter, a 1-km-long transect perpendicular to and 10 m away from the aforementioned leaf litter transects was established. At every 25 m, a 1-m² plot (for a total of 40 plots) was established and from each plot, all twigs potentially exploited as nests by ants were opened and checked for ants. All adults and brood were collected and stored in ethanol for identification and counting. All ant species sharing a twig were recorded, and the number of potential nests colonized was recorded. Potential nests are twigs that are hollow or catacombed, are within the size range normally used by ants (10–30 cm) (Byrne, 1994), and are fragile enough to be easily broken by hand. Twigs were counted as colonized only if they contained at least one queen, or if queenless, the twig had two or more workers with brood.

Artificial nests were made by drilling a 0.5-cm diameter hole lengthwise through wooden dowels (2 cm diameter × 9 cm long). The dowels were not chemically treated and were made from *Celtis latifolia*, a common tree species in the lowlands of New Guinea. The dimensions of these artificial nests mimicked twigs commonly used by ants as nests in nature (Byrne, 1994; Wilson, 1959), and previous studies have shown that ants in other parts of the world readily colonize these artificial nests (Byrne, 1994; Herbers, 1986; Kaspari, 1996a, b). We established a 1-km transect 15 m away from and parallel to the aforementioned control transect. Every 25 m along the transect, a 1-m² plot was established ($n = 40$). In each plot, five dowels were placed among existing natural twig nests and litter. After 2 months, all of the dowels were collected, with all colonizing ants counted and identified. Adults and brood found in the artificial nests were collected, stored in ethanol and later

identified and counted. The number of dowels colonized per plot was recorded.

A dissecting scope (10–30 \times) was used to identify, count, and sort ants into adults and non-adults. Then vouchers of each morpho-species were sent to Roy Snelling at the Los Angeles County Museum, LA, CA, USA, for species identification. Voucher specimens sent to R. Snelling are held in Los Angeles County Museum, and duplicates are deposited at the entomology section of the University of Papua New Guinea and PNG Institute of Biological Research entomology collections. Michaelis–Menton equations were used to estimate maximum species richness (S_{\max}) with an estimate of the sampling effort needed to detect 50% of the species (B). Species accumulation plots were calculated from each nest type using 999 permutations. Ant species composition of leaf litter, natural, and artificial twigs was compared using ANOSIM using Primer 6.1.11 software (Clarke and Gorley, 2006). First, a resemblance matrix was derived using Jaccard similarity coefficients, which was based on presence/absence data. Then comparisons between communities were conducted using 999 permutations and significance was assumed at $P < 0.05$.

The influence of nest density on ant species richness and abundance

The influence of naturally occurring potential nest material on the abundance and species richness of ants was examined using data from the above analyses. Spearman's correlation analyses were used to look for significant relationships between available natural twig nest number on the 1-km transect plots and species richness, the proportion of twigs colonized, and the total abundance of adult ants per plot.

To experimentally examine whether availability of potential twig nests affects the abundance and species richness of twig ants, we established another 300-m-long transect 15 m from and parallel to the previous 1 km artificial nest transect. Three 1-m² plots, each 5 m apart, were located every 30 m along this transect (for a total of ten sites, each with three plots). Potential artificial nests were placed at three different densities (low = 5, medium = 10, and high = 20) in each of the three plots and repeated at each site ($n = 10$ per treatment). All natural twigs from the plots were removed before adding the potential artificial nests; all other litter was left intact. To stabilize the number of evident “twigs”, control dowels (without lengthwise holes) were added to bring the number of “twigs” in each plot to 20 (combination of dowels with and without holes). Although it is difficult to know when twig-dwelling ants reach equilibrium in their nests, similar studies shows that 30–60 days is enough time for twig ants to colonize artificial nests (Kaspari, 1996b). After longer

periods ants will often leave occupied nests to find new sites, e.g., after 36–147 days in a study in Costa Rica (Byrne, 1994). Thus, studies with artificial nests involve a tradeoff between leaving sufficient time for colonization and risking that ants will start to vacate nests. Therefore, artificial nests were harvested after 60 days to maximize the chance of capturing maximum nest occupancy. All ants found within the dowels were preserved, counted, and identified. Kruskal–Wallis tests were used to examine for a significant relationship between the three treatments of artificial twig density and species richness, the proportion of twigs colonized, and the total abundance of adult ants.

Results

Artificial twig, natural twig, and litter ant communities

The most species-rich communities were observed in the leaf litter, followed by the natural twigs, with the artificial twigs having the lowest number of species (Fig. 1). Fifty-five ant species were captured: 32 from the leaf litter, 29 from naturally occurring twigs, and 12 from artificial nests (Table 1). The most frequently encountered species were: *Cryptopone butteli* Forel in the leaf litter (occurring in 21/40 plots) and *Pheidole* sp. O in both the natural twigs (occurring in 21/40 plots) and in the artificial twigs (occurring in 6/40 plots). A total of 23 species in 19 genera and 7 subfamilies occurred exclusively in litter, and 14 species in 13 genera and 6 subfamilies were captured exclusively in natural twig nests. An

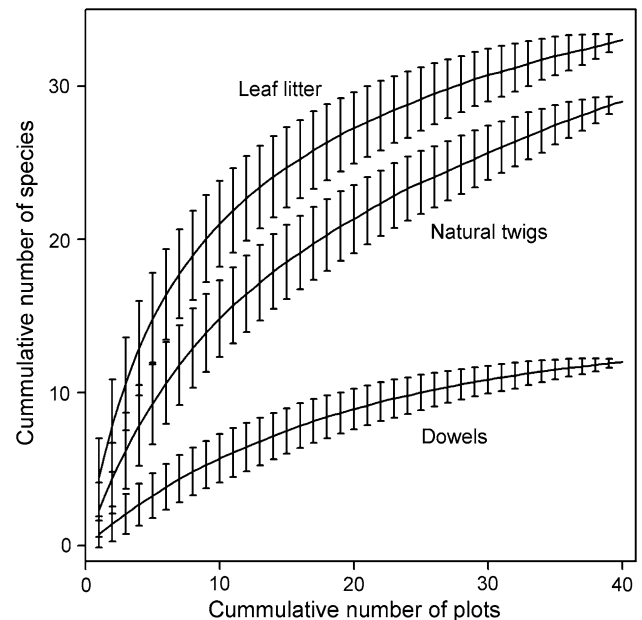


Fig. 1 Species accumulation curves for ants observed in leaf litter, naturally occurring twig nests, and artificial nests made from wooden dowels. Error bars are ± 1 SE

Table 1 Ant species in various nest types

Subfamily	Tribe	Species	Nest type		
			Litter (%)	Twigs (%)	Dowels (%)
Aenictinae	Aenictini	<i>Aenictus philiporum</i> Wilson 1964	2 (5)	0 (0)	0 (0)
Cerapachyinae	Cerapachyini	<i>Cerapachys pusillus</i> Emery 1897	5 (12.5)	2 (5)	0 (0)
		<i>Cerapachys</i> sp. B	0 (0)	1 (2.5)	0 (0)
		<i>Cerapachys</i> sp. C	0 (0)	1 (2.5)	0 (0)
		<i>Sphinctomyrmex cribratus</i> Emery 1897	2 (5)	0 (0)	0 (0)
Dolichoderinae	Dolichoderini	<i>Tapinoma</i> sp. A	0 (0)	1 (2.5)	0 (0)
Formicidae	Camponotini	<i>Camponotus</i> sp. A	0 (0)	1 (2.5)	0 (0)
		<i>Polyrhachis</i> sp. A	0 (0)	2 (5)	0 (0)
	Lasiini	<i>Acropyga</i> sp. A	5 (12.5)	0 (0)	0 (0)
	Plagiolepidini	<i>Paratrechina</i> sp. A	2 (5)	0 (0)	0 (0)
<i>Paratrechina opaca</i> Emery 1887		0 (0)	1 (2.5)	1 (2.5)	
Myrmicinae	Crementogasterini	<i>Crementogaster</i> sp. A	0 (0)	1 (2.5)	0 (0)
	Dacetini	<i>Strumigenys loriai</i> Emery 1897	4 (10)	2 (5)	0 (0)
		<i>Strumigenys ortholex</i> Bolton 2000	9 (22.5)	0 (0)	3 (7.5)
		<i>Strumigenys szalayi</i> Emery 1887	0 (0)	6 (15)	2 (5)
		<i>Strumigenys wallacei</i> Emery 1897	4 (10)	0 (0)	0 (0)
	Formicoxenini	<i>Cardiocondyla</i> sp. A	0 (0)	1 (2.5)	0 (0)
		<i>Xenomyrmex</i> sp. A	0 (0)	2 (5)	0 (0)
	Myrmecini	<i>Myrmecina</i> sp. A	1 (2.5)	0 (0)	0 (0)
		<i>Myrmecina</i> sp. E	1 (2.5)	0 (0)	0 (0)
	Pheidolini	<i>Pheidole impressiceps</i> Mayr 1876	7 (17.5)	0 (0)	0 (0)
		<i>Pheidole</i> sp. A	0 (0)	5 (12.5)	1 (2.5)
		<i>Pheidole</i> sp. B	1 (2.5)	0 (0)	0 (0)
		<i>Pheidole</i> sp. C	11 (27.5)	0 (0)	0 (0)
		<i>Pheidole</i> sp. L	1 (2.5)	0 (0)	0 (0)
		<i>Pheidole</i> sp. M	0 (0)	1 (2.5)	4 (10)
		<i>Pheidole</i> sp. N	0 (0)	1 (2.5)	3 (7.5)
		<i>Pheidole</i> sp. O	0 (0)	11 (27.5)	6 (15)
		<i>Pheidole</i> sp. P	0 (0)	2 (5)	0 (0)
		Solenopsidini	<i>Monomorium talpa</i> Emery 1911	1 (2.5)	0 (0)
<i>Oligomyrmex</i> sp. A			5 (12.5)	0 (0)	0 (0)
<i>Oligomyrmex</i> sp. B			0 (0)	8 (20)	3 (7.5)
<i>Oligomyrmex</i> sp. C	13 (32.5)		10 (25)	0 (0)	
<i>Tranopelta</i> sp. A	0 (0)	1 (2.5)	0 (0)		
Stenammini	<i>Rogeria</i> sp. A	0 (0)	6 (15)	0 (0)	
Tetramoriini	<i>Rhoptromyrmex</i> sp. A	9 (22.5)	0 (0)	0 (0)	
	<i>Tetramorium ornatum</i> Emery 1897	3 (7.5)	0 (0)	0 (0)	
	<i>Tetramorium vandalum</i> Bolton 1977	11 (27.5)	3 (7.5)	1 (2.5)	
Pheidologetonini	<i>Pheidologeton affinis</i> Emery 1900	3 (7.5)	0 (0)	0 (0)	
PONEROMORPHS					
Amblyoponinae	Amblyoponini	<i>Prionopelta opaca</i> Emery 1897	8 (20)	0 (0)	0 (0)
Ectatomminae	Ectatommini	<i>Gnamptogenys grammodes</i> Brown 1958	0 (0)	0 (0)	2 (5)
		<i>Gnamptogenys</i> sp. A	0 (0)	6 (15)	0 (0)
Heteroponeninae	Heteroponereini	<i>Heteroponera</i> sp. A	1 (2.5)	0 (0)	0 (0)
	Ponerini	<i>Brachyponera</i> sp. A	10 (25)	0 (0)	0 (0)

Table 1 continued

Subfamily	Tribe	Species	Nest type		
			Litter (%)	Twigs (%)	Dowels (%)
Ponerinae		<i>Cryptopone butteli</i> Forel 1913	21 (52.5)	0 (0)	0 (0)
		<i>Hypoponera sabronae</i> Donisthorpe 1941	16 (40)	0 (0)	0 (0)
		<i>Myopias tenuis</i> Emery 1900	3 (7.5)	6 (15)	1 (2.5)
		<i>Myopias</i> sp. A	0 (0)	3 (7.5)	0 (0)
		<i>Pachycondyla acuta</i> Emery 1900	8 (20)	1 (2.5)	0 (0)
		<i>Pacycondyla obscurans</i> Walker 1859	0 (0)	0 (0)	2 (5)
		<i>Pachycondyla rubra</i> Smith 1857	3 (7.5)	0 (0)	0 (0)
		<i>Pachycondyla</i> sp. A	0 (0)	3 (7.5)	0 (0)
		<i>Ponera</i> sp. A	3 (7.5)	0 (0)	0 (0)
Proceratinae	Probolomyrmecini	<i>Probolomyrmex</i> sp. A	2 (5)	5 (12.5)	0 (0)
	Proceratiini	<i>Discothyrea</i> sp. A	1 (2.5)	1 (2.5)	0 (0)

Both the total number of plots occupied by each species, and the relative percentage of the 40 plots occupied by each species are shown (in brackets)

additional six species in six genera occurred both in litter and natural twig nests (Table 1). Interestingly, two species (*Gnamptogenys grammodes* Brown and *Pachycondyla obscurans* Walker) were captured in artificial nests but not from natural nests or leaf litter.

Myrmicinae and Poneromorphs were the most species-rich groups occurring in both leaf litter and natural twigs, while Myrmicinae was the only species-rich group occurring in both natural and artificial nests (Table 1). *Tetramorium vandulum* Bolton and *Myopias tenuis* Emery occurred in the litter, natural twigs, and the artificial nests, whereas *Strumigenys ortholex* Bolton occurred only in the litter and the artificial nests. All species in Cerapachyinae, Dolichoderinae, and Formicinae occurred both in leaf litter and natural nests except for *Paratrechina opaca* Emery, which occurred in natural and artificial plots only. Michaelis–Menton equations estimated the maximum species richness to be 39 ($S_{\max} = 38.65$, $B = 8.06$), 40 ($S_{\max} = 39.65$, $B = 16.49$), and 20 ($S_{\max} = 19.98$, $B = 25.33$), in leaf litter, natural, and artificial twigs, respectively. The ANOSIM and the associated pair-wise comparisons indicated that each of the three nest types had a significantly different species composition (Global $R = 0.232$; $P < 0.001$). The relatively low Global R estimate indicated that there is considerable overlap in the species occurring in these samples, but P value indicates that the communities were not exactly the same. A significant but substantially lower R statistic was still observed in an examination of pair-wise tests between species observed in dowels and natural twigs ($R = 0.079$; $P < 0.001$).

Multiple ant species were commonly observed to share the same twigs or dowels. Fourteen ant species colonizing natural twig nests were found occupying the same natural nest as another species, and 19% of natural twigs were

colonized by more than one ant species (Table 2). In artificial nests, four ant species cohabited dowels with another species, and 8% of occupied dowels were colonized by more than one ant species. *Oligomyrmex* sp. B, one of the most abundant ant species shared nests with six other ant species followed by *Pheidole* sp. N which shared nests with five other ant species.

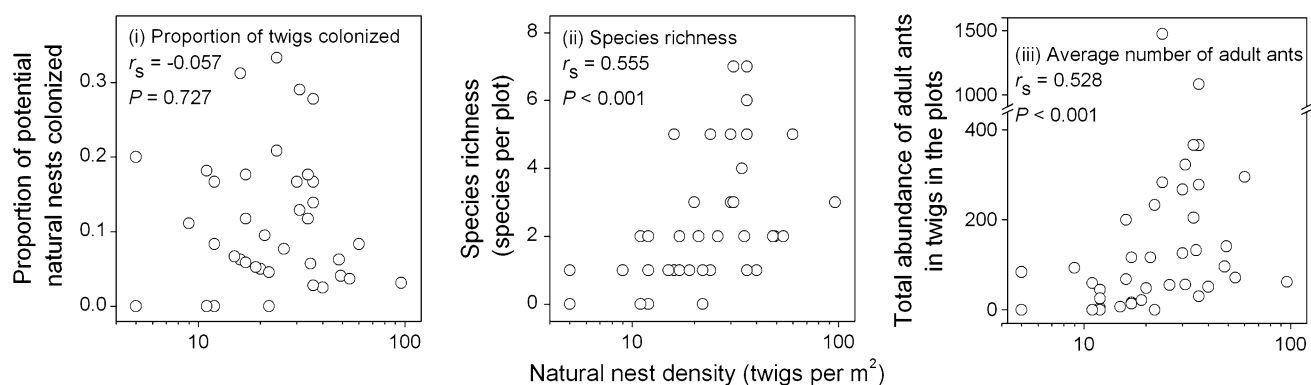
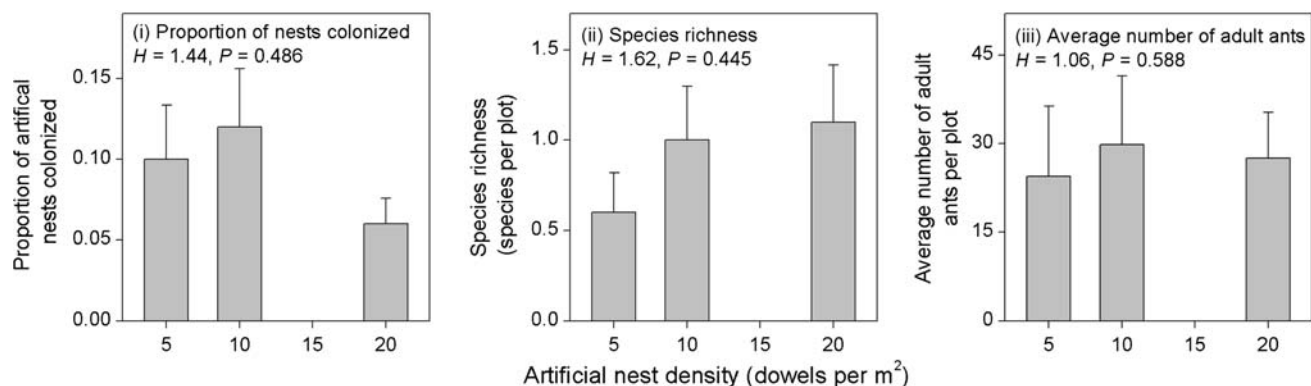
The influence of nest density on ant species richness and abundance

The density of naturally occurring twigs varied considerably among the 1-m² plots. The median number of twigs per plot was 23 (range 5–96) (Fig. 2). The proportion of potential nests colonized was generally low, with an overall mean colonization rate of 11.2% of twigs that we considered suitable for ant nests. The colony size (queen and workers) of each species per nest ranged from 1 to 184 in artificial nests, compared to 1–612 ants in natural twig nests. There was no significant relationship between the number of twigs per plot and the proportion of twigs colonized by ants ($P = 0.727$). However, both species richness and the total abundance of adult ants (both worker and reproductive forms) were significantly positively correlated with increasing density of naturally occurring twigs ($P < 0.001$; Fig. 2).

Increasing the availability of artificial nests from 5 to 20 dowels per plot had no significant effect on the proportion of artificial nests colonized, species richness, or total colony size ($P \geq 0.445$; Fig. 3). The overall colonization rate for these artificial nests was 9.16%, which is comparable to the 11.19% observed in natural twigs. Mean species richness in the artificial nests increased from 0.60 ± 0.22 (SE) in plots with 5 dowels to 1.10 ± 0.31 (SE) in plots with 20

Table 2 Species that co-occurred together within the same twig or dowel (artificial nest)

Species	Shared nest with	Number of nest shared	Nest type
<i>Pheidole</i> sp. N	<i>Camponotus</i> sp. A	1	Twig
	<i>Strumigenys szalayi</i>		Twig
	<i>Polyrhachis</i> sp. A		Twig
	<i>Strumigenys ortholex</i>	2	Dowel
	<i>Pheidole</i> sp. O	1	Dowel
<i>Rogeria</i> sp. A	<i>Pheidole</i> sp. P	1	Twig
	<i>Oligomyrmex</i> sp. C		Twig
	<i>Pheidole</i> sp. A	1	Twig
<i>Oligomyrmex</i> sp. B	<i>Probolomyrmex</i> sp. A	1	Twig
	<i>Strumigenys szalayi</i>		Twig
	<i>Rogeria</i> sp. A		Twig
	<i>Pheidole</i> sp. O	1	Dowel
<i>Gnamptogenys</i> sp. A	<i>Cardiocondyla</i> sp. A	1	Twig
	<i>Cerapachy</i> sp. A		Twig
	<i>Probolomyrmex</i> sp. A		Twig
	<i>Tranopelta</i> sp. A	1	Twig
	<i>Oligomyrmex</i> sp. B		Twig
<i>Pheidole</i> sp. A	<i>Gnamptogenys</i> sp. A	1	Twig

**Fig. 2** The influence of natural twig density on: (i) the proportion of natural twigs colonized by ants, (ii) ant species richness, and (iii) the average number of adult ants (adult males and females, including queens). P values and r_s values are from Spearman's rank correlation analyses**Fig. 3** The influence of artificial twig (wooden, drilled dowels) density on (i) the proportion of artificial twigs colonized by ants, (ii) ant species richness, and (iii) the average number of adult ants (adultmales and females, including queens). P values and H statistics are from Kruskal–Wallis tests. Error bars are ± 1 SE

dowels, but in each treatment there were multiple plots in which none of the dowels had been colonized.

Discussion

We hypothesized that abundance and diversity of twig-dwelling ants would be positively correlated with greater nest availability. This hypothesis was supported in the natural twig assembly ($P < 0.001$), though not in our experiments with artificial nests ($P = 0.445$). Similar patterns were observed in adult ant abundance. There are likely to be several reasons for these contrasting results. First, the communities forming in the artificial dowels were significantly different from those in naturally occurring twigs. This is not surprising because a diverse array of twigs can attract more ant species than twig nests from single species of tree (Armbrecht et al., 2004). Here, artificial dowels were made from single tree species. The difference in the quality (microclimate conditions, food items, number of cavities) of the artificial dowels and natural twig nests may be responsible for the differences in diversity and abundances between these two twig types. Even though this was not significant, the correlation analysis used for natural twigs was more powerful in detecting trends than was the Kruskal–Wallis which tests for differences in median rates of colonization in dowels. Second, the maximum density of natural twigs (96) far exceeded the highest density of artificial nests we employed (20) suggesting that greater nest density or diversity of natural twigs may have allowed for greater species richness (Armbrecht et al., 2004). Species richness had not reached a plateau even at the highest levels of natural twig density. Nevertheless, species were shared between the two systems, and there was a definite trend for increasing species richness with increasing artificial nest density.

The overall mean rate of potential twig use was 9–11%, which is similar to that observed in other studies (Byrne, 1994; Kaspari, 1996b). In the natural twig communities, one plot had eight occupied nests in a total of 24 potential twigs. In another adjacent plot, there were no colonies in 22 potential twigs. Clearly, there was substantial variation in the utilization of natural or artificial nest sites among plots. This variation is possibly a function of experimental design and/or function of both biotic and abiotic factors. Two months of colonization may have not been long enough for litter ants to reach full colonization in artificial nests as evidenced by only one-third of the twig-dwelling ants colonizing the artificial nests. Poor colonisers may need more time to colonize artificial nests as species richness and composition in litter can take longer than 2 months to recover after the litter has been disturbed (Campos et al., 2007). Despite high density of potential twig-nests, perhaps

only a subset is suitable for colonization because twigs have an estimated life span of 264 days (Byrne, 1994) on the forest floor. During this time twigs are probably uninhabitable because freshly fallen and thoroughly decayed twigs are not suitable for nesting (Herbers, 1986). Biologically, army ants can cause significant disturbance to litter ant communities (Franks, 1982; Franks and Bossert, 1983; Hölldobler and Wilson, 1990; Rettenmeyer, 1963). Seven species of army ants occur in New Guinea (Snelling, 1996), and the presence of army ant (*Aenictus philiporum* Wilson) in this study may have strong influence on the community structure of the twig-dwelling ants. Competition for resources is a major factor structuring ant communities (Hölldobler and Wilson, 1990; Holway, 1999); therefore, other dominant ant species may influence community assemblages as they do in mangrove ant communities (Cole, 1983) or tropical islands (Lester et al., 2009).

The different ant communities formed in leaf litter compared to twigs (Table 1) are not surprising because different species have different nesting requirements. For example, many leaf litter ants use other vegetal matter such as leaves, fruits, seeds, barks, and cracks in the rocks as nesting resources (Soares and Schroeder, 2001). However, because litter and twigs are found in the same habitat, it is expected that some ant species such as *Strumigenys ortholex* Bolton, *Tetramorium vandalum* Bolton, and *Myopias tenuis* Emery were found in both litter and twigs. The total number of twig-dwelling ant species captured in this study (32) is the same as total number of ant species found in a forest in Costa Rica (32) that used similar study methods (Byrne, 1994). Only nine of the twig-dwelling species colonized artificial nests in PNG (29%) and only 13 species did in Costa Rica (41%). The lower species diversity of the ant fauna in artificial dowel nests versus natural twig nests in these two regions perhaps reflects a general trend though it could also mean that the 2-month study period was not long enough for litter ants to reach full colonization in artificial nests, or it may also reflect the relatively simple habitat of the artificial nests (each having a similar sized nest entrance, etc.) relative to the diversity of habitats provided in naturally occurring twigs (Armbrecht et al., 2004).

One of the most interesting aspects of the study was the coexistence of multiple ant species within twigs. Nest sharing in twig-dwelling ants is rarely reported despite much interest in tropical litter ant ecology (Byrne, 1994). Here, we report this rarely observed phenomenon, where 50% (16 of 31) of the twig-dwelling ant species shared both natural and artificial twig nests with another species (Table 2). Although this study was not designed to study resource partitioning among twig-dwelling ants, the coexistence of different ant species in the same twig may suggest that nests are not strongly partitioned at least among these species, a conclusion drawn in a similar study

(Byrne, 1994). In this study, *Oligomyrmex*, *Pheidole*, and *Strumigenys* occupied more nests than other ant groups and shared nests with many ant species. *Pheidole* and *Strumigenys* are general scavengers and predators of other invertebrates, while *Oligomyrmex* and *Cerapachys* are specialist predators of other ant species (Greenslade, 1979; Hölldobler, 1982). However, we still found different ant species sharing nests, which suggest that these other ant species must not be prey species or these species sharing nests presumably do not involve in territorial conflicts. There might at times be an advantage to sharing a nest, such as mutual defense of the twig from shared predators.

Twigs, by definition, are important to twig-dwelling ants. While we observed that species richness and ant abundance increased with natural twig density, just why so many potential twig nests remain vacant and available for ant colonization is unknown. We suspect that population level of litter ants are kept at low level by parasites such as phorid flies (Morrison, 1999, 2000), fungal infection (Briano et al., 1995) or predation by other ants (Franks and Bossert, 1983) and other dominant ant species. Constant disturbance to the litter ant communities from twig and other vegetal fall, torrential rain and scrubbing, and shifting of litter by animals (e.g., pigs and wild fowl) may force ants to relocate their nests frequently as disturbance can influence litter ant communities significantly (Campos et al., 2007; Kaspari, 1996a). During nest relocation and colony founding alātes and colonies face high mortalities (Hölldobler and Wilson, 1990) which may lead to low utilization of resources. The low utilization of potential twig nests in this study was also observed in Neotropical litter ant communities (Byrne, 1994; Kaspari, 1996a, 1996b) which suggests that availability of twigs alone probably does not strongly shape the litter ant communities.

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