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TECHNIQUES & METHODOLOGY

Rapid assessment of the three-dimensional distribution of dominant arboreal ants in tropical forests

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Abstract. 1. Ants are omnipresent in tropical forests, especially territorially dominant arboreal ants whose territories are spatially segregated forming 'ant mosaics'. These ecologically important species are rarely used in conservation monitoring because of the difficulty in collecting them. We developed a standardised baitline protocol to study the distribution of dominant ants on canopy trees and also a procedure to objectively define species dominance, even in unknown ant assemblages.

2. Besides eliminating the need to climb trees, this protocol allows live arboreal ant specimens to be sampled at different heights. Behavioural aggressiveness assays between the collected workers provide data on the three-dimensional distribution of colonies and on interactions between species. We compared the results of the behavioural tests to those from null models.

3. In the New Guinean lowland forest studied, we show that the canopy was either shared by multiple territorial species or inhabited by a single species with a large territory. The baitline protocol collected up to half of the arboreal ant species found in a felling census. However, the proportion of species collected at baits decreased with the increasing spatial dominance of single territorial species.

4. Behavioural observations used in the protocol allowed a more efficient detection of ant mosaics than null models. Territorially dominant ants were active on both understorey and canopy trees.

5. The protocol is fast and easy to replicate. It is a potential tool for understanding and monitoring the spatiotemporal dynamics of arboreal ant assemblages and can detect populous colonies, including those of invasive species.

Key words. Ant mosaics, canopy, competition, C-scores, dominant arboreal ants, null models, Papua New Guinea, primary forests, stratification, territoriality.

Introduction

Vegetation stratification in lowland tropical rainforests (i.e., emergent, canopy, sub-canopy, and understorey strata) is the major factor affecting arthropod species distribution and abundance with a greater impact than seasonality or geographical distance (Basset *et al.*, 2015). This stratification affects the distribution of ants that are one of the most abundant arthropod groups in these forests both in terms of biomass and number of individuals, so that their ecological impact is particularly high in tropical rainforests (Ryder Wilkie *et al.*, 2010; Floren *et al.*, 2014; Longino & Colwell, 2020; Leponce *et al.*, 2021). This high abundance of arboreal ants is possible because most species are partly herbivorous feeding on extrafloral nectar, food bodies, pollen, sap and, particularly, on hemipteran honeydew (otherwise referred to as 'cryptic herbivores') (Davidson *et al.*, 2003; Hunt, 2003). Actually, most of these ants are generalists as they also scavenge dead animals and faeces and capture

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different kinds of prey (Blüthgen *et al*., 2000; Floren *et al*., 2002).

Some arboreal ant species are both numerically and behaviourally dominant in tropical rainforest canopies where they defend territories inter- and intra-specifically. These territorially dominant arboreal ants (territorial ants hereafter) build large and usually polydomous nests that may extend to multiple trees (Dejean *et al*., 2007). The mutual exclusion of these territorial ants from tree canopies leads to a patchy three-dimensional distribution of the territories called 'ant mosaics' that were first described for tree crop plantations which are lower and structurally simpler than rainforests (Room, 1971; Majer, 1972; Leston, 1978; Armbrecht *et al*., 2001; Blüthgen & Stork, 2007; Dejean *et al*., 2007; Adams, 2016). According to the concept of the ant mosaic, non-dominant species can be tolerated or negatively or positively associated with territorial ants (Majer, 1972). Consequently, territorial ants affect the distribution of other ants in tree canopies through competitive interactions or by affecting colonisation or colony founding processes (Philpott, 2010). They also maintain mutualistic relationships with hemipterans or myrmecophytic epiphytes and most of them are fierce predators sometimes used in biological control (Dejean *et al*., 2007). Despite their impact on the abundance and distribution of other organisms, territorial arboreal ants are rarely used in insect conservation monitoring because of the difficulty in collecting them, especially in rainforests (Underwood & Fisher, 2006).

There are four major arboreal ant collection methodologies. First, various climbing-based collection methods include visual search, arboreal baits, arboreal traps, vegetation beating, epiphyte inspection, and branch clipping (Antoniazzi *et al*., 2020; Delabie *et al*., 2020). Second, canopy fogging, which consists of spraying an insecticide, usually pyrethrum, into the tree crowns using a fumigator is very useful for the study of ant species richness (Floren *et al*., 2014; Yusah *et al*., 2018). Third, methods relying on a construction crane to reach the upper levels of the canopy allow researchers to collect detailed information on the biology of the species (Blüthgen & Fiedler, 2004). Fourth, opportunistic collections can be conducted on trees felled when villagers establish their plantations. This method can be used to carry out a species census including detailed information on nesting sites, species abundance, and the ant species associated with each tree by differentiating ant foragers from nesters (Klimes *et al*., 2012; Volf *et al*., 2019).

To detect territorial ant species and the mosaic pattern of their territories, most studies have relied upon indirect evidence using statistical methods based on species co-occurrences or correlations between species abundance, not behavioural observations or the marking of individuals. The purpose of these statistical methods is to examine the ways (i.e., negative, neutral, or positive) in which species are associated. This segregation, aggregation, or indifference can be measured at the scale of a plot with replicated samples (typically individual trees) and for all ant species sampled, for only numerically dominant species, or for a set of selected species taken pairwise (Pfeiffer *et al*., 2008; Law & Parr, 2020). The tendency for species to exclude one another is interpreted as an indication of the presence of a mosaic. *Chi*-square independence tests were firstly used (Leston, 1973; Majer *et al*., 1994; Blüthgen & Stork, 2007), but, subsequently, the use of null models became widespread. Null models compare observed species co-occurrence on trees with randomised matrices of species co-occurrences used as benchmarks to determine if the observed pattern of exclusion is more or less frequent than observed by chance (Gotelli & Graves, 1996). One difficulty with using these models is that their result depends on both the randomisation algorithm and the size of the matrix; that is, the selection of the species considered (the entire assemblage or the most common species) and/or the sampling scale (Blüthgen & Stork, 2007; Dejean *et al*., 2007). In addition, species co-occurrence models often assume the spatial independence of species occurrences (Gotelli & Ulrich, 2012).

We had three research objectives: (i) To provide a reproducible rapid assessment protocol, namely the *standardised baitline protocol* (SBP), designed to detect dominant arboreal ants, the associations between them and the three-dimensional extension of their territories (i.e., vertically, along tree trunks, or horizontally across neighbouring tree crowns). The protocol eliminates the need to climb by sampling ants on upper canopy trees with baits positioned at regular intervals on a rope operated from the ground and running along the trunks. Aggressiveness tests for dominant species were conducted. Interspecific confrontations were set up to verify if there is exclusion and intraspecific confrontations (workers gathered from different trees) to determine the extent of their territories. (ii) To evaluate the representativeness of the baitline method in terms of arboreal species richness in relation to species dominance (which may result in the exclusion of other species at the baits; Parr, 2008), we compared the observed species richness of three SBP plots that reflect an increasing degree of dominance of territorial ants with that of a complete survey in a plot of a similar size. (iii) To demonstrate the utility of the baitline method to study interspecific interactions and to detect the presence of ant mosaics we compared the results of our direct (observational) approach based on aggressiveness tests and the co-occurrence of species at the baits with the indirect approach based on null models using C-scores (i.e., presence–absence of species in trees). The sensitivity to sample size of indirect methods is further discussed by considering various combinations of trees sampled by baitlines or by the complete survey in the same forest plain.

Materials and methods

Presentation of the SBP

Sampling design. The protocol is illustrated in Fig. 1 and Fig. S1 and an accompanying video is in Appendix 1. We used a slingshot to place an arborist throwline with a weighted bag on one end over a top branch on each selected tree (Fig. 1c). Thanks to its weight, the bag pulls the throwline to the ground on the other side of the branch. Then, after removing the weighted bag, we tied a polyamide rope to that end of the throwline and pulled on the other end until the rope created a large loop between the ground and the top branch (Fig. 1d,e). As it can be pulled back and forth, this rope permitted us to position the baits along the tree trunks and later to lower them gradually to inspect these baits (Fig. 1f,g). The baits were positioned along the tree

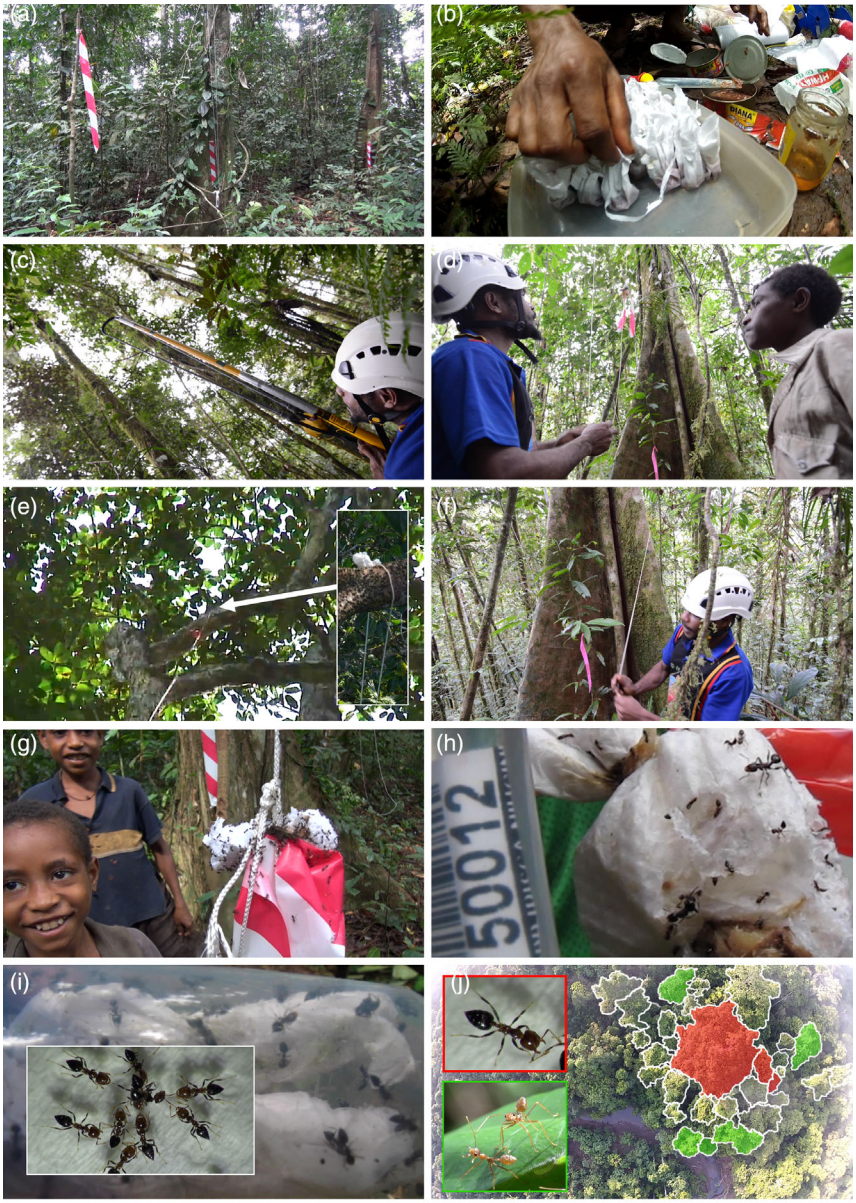

Fig 1. The standardised baitline protocol explained step by step. Plot and tree marking: (a) Around the central tree (labelled #1), all the trees forming the upper canopy (exposed to direct sunlight) are selected within a 30 m radius. Bait preparation: (b) Tinned fish (100 gr) is mixed with two soup spoons of honey (syrup can be used alternatively if bees are attracted and expel ants from the baits). A teaspoon of the mixture is placed on a paper towel (10 × 20 cm approx.). The paper towel is folded to form a small bag containing the food. Installation of the ropes in trees: (c) an arborist throwline attached to a throw bag is slung into the canopy of each tree selected using a giant slingshot. Safety equipment (helmet, security glasses, and gloves) must be worn during this operation. The arborist throw line is replaced with a standard rope. The two ends of the rope are attached together, forming a loop. (f) The loop is twisted around the tree trunk (see also Fig. S1a). (d) Baits are installed by pulling the rope. They must be in direct contact with the tree. (e) The uppermost bait is installed at the junction of the beginning and end of the rope forming the loop. Baits are installed every 5 m (2, 7, 12, 17 m and over, depending on the tree height). (f) The loop is twisted around the tree trunk. (g) Baits are installed in the morning and collected in the afternoon (4 h later). They sometimes attract a large number of ants (here *Crematogaster polita*). This number is estimated and noted. (h) Voucher specimens are collected from each bait. When several species are found together on a bait they are placed in the same vial (here *Crematogaster muralti* Forel, 1910 and *Atopomyrmex mocquerysi* André 1889 in DR Congo). (i) In situ aggressiveness tests: Confrontation tests between individuals collected from different locations can be organised in the field to delineate the extension of territories or to confirm interspecific antagonism. The occurrence of individuals fighting is considered proof of agonistic behaviour (inset). (j) Baitlines are useful in deliminating the three-dimensional (i.e., vertical and horizontal) segregation of mutually aggressive dominant ants, here *Cr. polita* and *Oecophylla smaragdina*. See also the companion video in Appendix 1.

trunks every 5 m, starting from 2 m above the ground. Each bait height was verified with a laser range finder monocular (Trupulse® 360R). If needed, baits were shifted along the rope in order to be at the right height and touching the tree. They were made of a mixture of honey and canned fish in oil wrapped in small pieces of paper towel (Fig. 1b), attracting a wide range of ant species (Law & Parr, 2020) and were left for 4 h before being collected. This allows the bait to be installed in the morning and collected in the afternoon (see Appendix 2). The baits, distributed on only one side of the line, were gradually brought back, starting from the closest to the ground. One of the keys to the success of this method is that the ants remain on and inside the bait when it is brought back for inspection (Fig. 1g). We observed that ants are apparently little disturbed when pulled down from tree and rarely fall from the baits (as verified during preliminary tests with a large collecting sheet on the ground).

Because it is practical, we used circular plots centred on a large tree to map the distribution of the ants (Fig. S1). A radius of 30 m (0.28 ha) generally includes a substantial number of canopy trees (here, 27–31) and can be studied fairly quickly (3 days during a warm, dry period by a team of four people, see Appendix 2) (Fig. S1). The upper canopy and emergent trees, all exposed to direct sunlight, were chosen for sampling because they are the most likely to host territorial ant colonies (Ribeiro *et al*., 2013). Ant specimens were taken from each bait for subsequent identification. The number of individuals present on the bait was counted or, when greater than 10, categorised into two classes (average abundance up to 20 or high abundance above 50 workers, see Table S1). The coordinates, the circumference and the height of each tree were recorded using a compass, a measuring tape and a rangefinder (Fig. S1c,d). Trees were labelled and photographed (trunk and crown) for future reference. On trees where no ants were collected, the baiting was replicated to confirm the absence of ants. If needed, baits were put back into place to collect more individuals for aggressiveness tests (see below). The list of equipment and consumables required is presented in Fig. S2.

Procedure to objectively define species dominance. Our baitline protocol allows species to be mapped both horizontally (i.e., aerial view, Figs. 1j and 2a) and vertically (i.e., from ground to tree crown, Fig. 2b) to show their three-dimensional distribution across trees. For each plot mapped, the ant species are divided into three foraging activity categories according to their abundance at the baits and spatial distribution in the plot (Table 1): arboreal-foraging ants abundant at baits (category 1; Fig. 2a,b); arboreal-foraging ants not abundant at baits (category 2; Fig. 2c,d); and ants foraging only near the ground (category 3; Fig. 2e,f). This categorisation is accompanied by a coding system to compare the foraging behaviour of each species at different sites. The code includes the species frequency in the plot (number of trees occupied divided by the total number of trees), its foraging stratum (i.e., arboreal or near the ground), abundance at baits and vertical distribution along the tree. This helps to quickly identify territorial ants (see Table 1 for details and Table S2 for examples). In the rest of the text, we will define species as *frequent* when they are present on at least 10% of the trees studied, *dominant* when they are both frequent, abundant at baits and with a wide vertical distribution along the trees (according to the definitions in Table 1). *Territorial* species are defined as the dominants defending their foraging area from other species as demonstrated by aggressiveness tests.

Inter- and intraspecific aggressiveness tests (i.e., direct approach to detecting ant mosaics). Interspecific tolerance was noted when two species coexisted peacefully on the same bait (Fig. 1h). Interspecific aggressiveness was noted by examining the baits or when observing a clear spatial segregation between two species. Also, a key advantage of the SBP method is that aggressiveness tests can be conducted in the field, here by transferring the workers of one species to the territory of another.

For dominant ants, intraspecific aggressiveness tests can permit to identify which trees from each plot belong to the same territory and to draw maps of the extent of the territories. Each test was based on the encounter between two groups of workers gathered with the baits from two different trees using pairwise combinations. In the absence of aggressiveness, the workers were considered to belong to the same colony, so that the host trees were connected by a continuous line in Fig. 2a; if not, they were considered to belong to two different colonies. The following protocol was used. First, baits with numerous conspecific workers gathered from each tree were put into a numbered container. Second, small pieces of paper towel were added to these containers and left for at least 1 h, allowing the ants to get used to them. Third, using forceps, we gently transferred two pieces of paper towel with an equivalent number of ants (about 20), each group of ants coming from a different tree, into a neutral arena consisting of a new container. After each use, the forceps were cleaned with pure ethanol to avoid transferring the ants' colony odours or landmarks to the other pieces of paper. The results of the aggressiveness tests noted during worker encounters on the neutral arena were used as a binary character: aggressive (i.e., lunging, biting, pulling, or prolonged fighting) or not (i.e., indifference, antennations, or avoidance) (Suarez *et al*., 1999). Because aggressiveness is not always clear after the first encounters but can become evident later with the presence of fighters or corpses (Fig. 1i), the data gathered on the workers' behaviour 1 h after the confrontations was used to categorise the behaviour. In case of unclear behaviour (e.g., unusually prolonged antennations but no fights), new assays were carried out.

Study sites

During the 'Our Planet Reviewed – Papua New Guinea' project (Leponce *et al*., 2016, 2020), ants were sampled according to the SBP in three 0.28 ha plots, namely 'SBP1' (S5.22562°, E145.08190°, Wanang Conservation Area, 31 trees sampled 2–4 May 2013), 'SBP2' (S5.13804°, E145.77242°, Baitabag village, 30 trees sampled 9–11 June 2011), and 'SBP3' (S5.73499°, E145.33223°, Kausi, 27 trees sampled 16–18 March 2012). As a basis of reference for the local diversity of arboreal ants, we used the results of a complete survey of a 'whole forest' (WF) plot of 0.4 ha (40 × 100 m, 472 trees; Fig. S3a,b). This WF plot is an extension of the 0.32 ha plot presented in Klimes *et al*. (2012) conducted near Wanang (S5.2313°, E145.1822°) where all trees with a diameter at breast height (DBH) ≥5 cm had been felled for

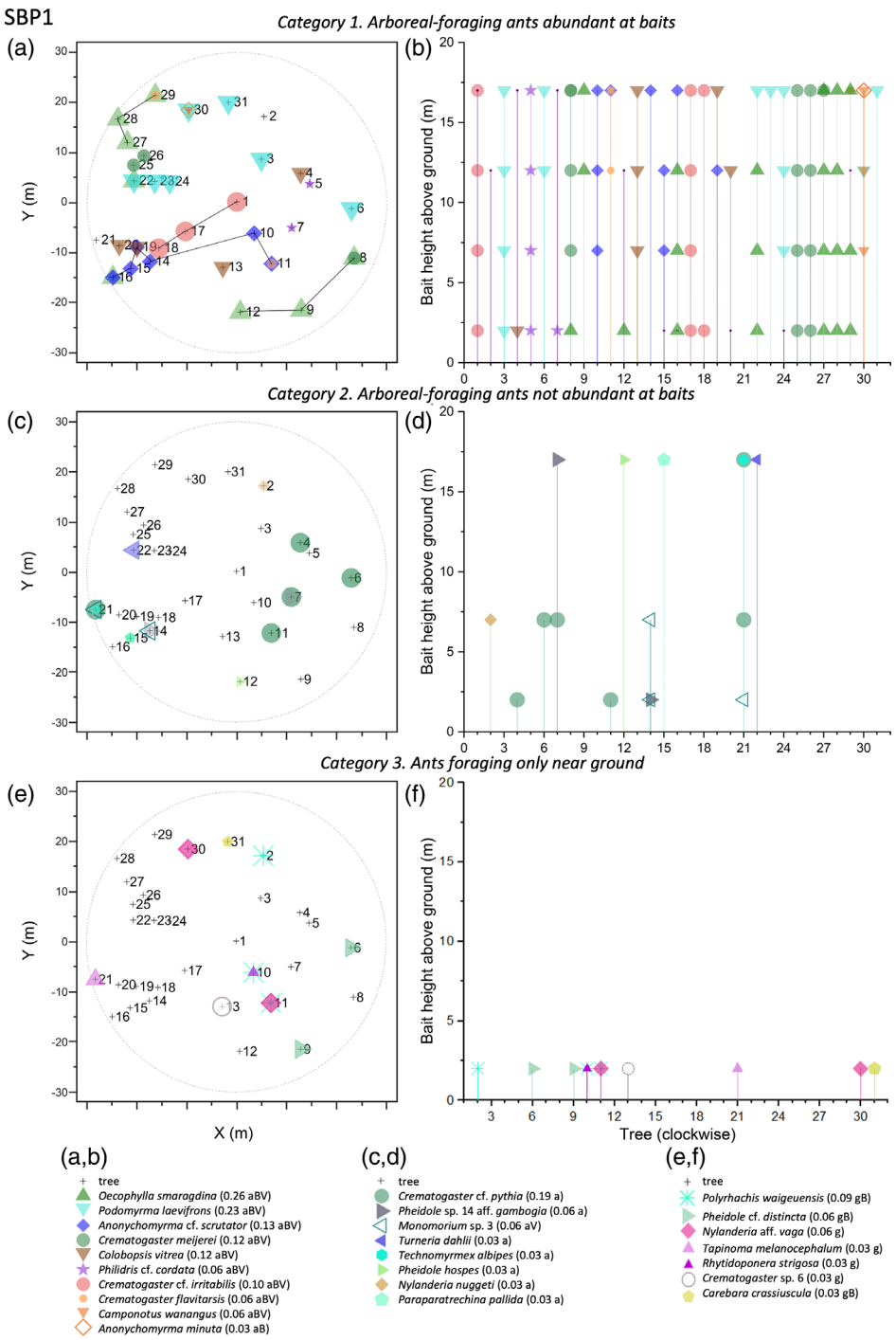

Fig 2. Plot SBP1 (31 trees). Maps of the horizontal (on the left) and vertical (right) distribution of three categories of ants according to their abundance and vertical distribution on baits (defined at plot level). (a,b) Category 1: arboreal-foraging species, dominant at baits and with a large vertical foraging area in the trees. They are called dominant arboreal ants if on at least 10% of the trees and territorial if defending their foraging area from other species. (c,d) Category 2: other arboreal-foraging ants, non-dominant at baits. (e,f) Category 3: ants foraging only near the ground. Continuous lines connect trees occupied by the same ant colony according to behavioural tests. Ant species names are followed by the frequency of the species in the plot and by a code describing its foraging activity in the plot: 'a' versus 'g': arboreal versus ground, 'B' dominant at baits, 'V': present on several baits (see Table 1 for details).

Table 1. Plot-based categorisation of ant species foraging activity into three categories. These categories quickly filter out species that do not have the characteristics of territorially dominant arboreal ants. A combination of three letters (from 'aBV' to 'g–') describes the ant foraging activity on individual trees. Category 1 includes ants foraging high in trees and in large numbers on the baits (≥10 workers per bait) (combinations 'aB'). If they occupy multiple baits at various heights above the ground ('V' suffix) and occupy at least 10% of the trees, they are called *dominant arboreal ants*. If dominant ants aggressively exclude each other from trees or parts of trees (see Figs. 1a,b and 2), they correspond to *territorial* ants (aBV). Category 2, non-dominant arboreal ants, concerns arboreal-foraging ants but observed in smaller numbers on baits (< 10 workers per bait, codes starting with 'a' not followed by 'B') (see Fig. 1c,d; Fig. S3a,b). Category 3 includes ants found only foraging near the ground (codes 'g' with optional 'B' suffix) (see Fig. 1e,f; Fig. S3c–f). These acronyms are used in combination with the species frequency in each plot, calculated by dividing the number of trees on which it was recorded by the total number of trees in the plot; for example, 0.19 aBV for *Anonychomyrma cf. scrutator* in plot SBP1 (see Table S1).

Category	'a' or 'g' max. bait height where observed	'B' dominant at baits (>10 individuals)	'V' vertical extension per tree (m)	Full abbreviation	If aggressive exclusion
1. Arboreal-foraging ants dominant at baits	>2 m: 'a'	Yes: 'B'	>0 m: 'V'	aBV	Territorial
			0 m: ''	aB	
2. Arboreal-foraging ants not dominant at baits		No: ''	>0 m: 'V'	aV	
			0 m: ''	a	
3. Ants foraging only near ground	≦2 m: 'g'	Yes: 'B'	–	gB	
		No: ''	–	g	

cultivation (Klimes, 2017; Volf *et al*., 2019). Once a tree was on the ground, the ants occupying it were collected by carefully dissecting all of its parts and inspecting all epiphytes and suspended soils. This allowed us to sample virtually all ant species, including their foragers and all their nests (see detailed protocol in appendix to Volf *et al*., 2019). A subset of canopy trees (WF26) was extracted from this large dataset to be compared with SBP plots (see below). All four sites were located in a primary evergreen tropical rainforest in the Ramu River basin of Papua New Guinea, (Whitfeld *et al*., 2014) and were separated from each other by 6–82 km. The average temperature was about 27°C, the average annual rainfall 3500 mm and the altitude 100–200 m (Leponce *et al*., 2016). There is little seasonality with a period of greater rainfall in December and January (McAlpine *et al*., 1975) during which we did not sample.

Representativeness of the baitline protocol in terms of arboreal species richness in relation to species dominance

The species richness in plots SBP1-3, increasingly dominated by territorial ants, was compared to the average richness of a subset of trees in the WF plot that most closely corresponded to the canopy trees targeted by the baitline protocol (i.e., 26 trees of the 472 in total, WF26 dataset) (Fig. S3c,d). For the sake of comparability, it was also verified beforehand that the richness of this WF26 dataset is representative of the average richness of all trees with a crown starting above 15 m in this plot. Rarefaction curves were calculated on the basis of ant species occurrence (presence/absence) on canopy trees with EstimateS 9.1 software (Colwell, 2013) with 100 randomisations of the sampling order without replacement.

Null model approach to detecting ant mosaics and its sensitivity to sample size

In plots SBP1-3, we studied species interactions between dominant species through behavioural observations. This approach was compared with the results from null models and the C-score index (Stone & Roberts, 1990) based on presence/absence data. As pointed out by Blüthgen and Stork (2007), the statistical power of the tests depends on the ant species occurrences and the number sampling units (trees). Therefore, we first excluded ant species that were infrequent because they were not indicative of any association between species. To enable meaningful statistical comparisons, we only conducted the tests on frequent species and with the additional condition that they occurred on at least three trees. Then, to further explore the effect of sample size we compared the results of C-scores on a large dataset (WF) (Fig. S3a,b) and on its subset of 26 emergent and upper canopy trees (WF26) comparable to the one targeted by the standardised baitline (Fig. S3c,d).

The C-score index measures the average number of checkerboard units between all possible species pairs (Gotelli, 2000). A higher or lower observed C-score than expected by chance suggests that the assemblages are predominantly structured by negative or positive associations between species, respectively. In ant mosaics, negative associations can be expected to predominate due to competitive exclusions. We used a randomisation algorithm that maintains the species occurrence frequencies and considers all trees equiprobable (SIM2 in Gotelli, 2000 because it has good statistical properties (not prone to false positives) and is recommended for the study of patterns of association in ant assemblages (Gotelli, 2000; Dejean *et al*., 2007). SIM2 is ecologically plausible here as our focal trees were of similar heights; but see Plowman *et al*. (2019) for tree-size dependent tests. All computations were made using R (RCoreTeam, 2019) and EcoSimR package (Gotelli *et al*., 2015). For each plot, matrices of ant × trees with presence/absence data were created and species co-occurrences were calculated at two scales: first, at the assemblage scale (global pattern) with the C-score index calculated on the assemblage of frequent species; and, second, between frequent species taken pairwise. The standardised effect size was calculated as SES = (observed index – mean of simulated index)/standard deviation of simulated index. A Šidák correction (Šidák, 1967)

Table 2. Plot characteristics and C-score analysis of co-occurrence patterns of ants. The ant species categories refer to Table 1 that filters species according to their dominance on baits and trees at the plot scale in order to detect territorially dominant ants. C-scores were calculated at the plot scale using the most frequent ant species (i.e., if they occupied at least 10% of the trees). The C-score analysis is not relevant in the case of SBP3 where all trees but one were occupied by a single species. See Materials and Methods for more details about the randomisation of the C-scores.

		Ant species					C-scores					
Plot	N trees	All	Cat.1	Cat.2	Cat.3	Frequent	Observed	Estimated	sd	SES	Significant	Pattern
SBP1	31	25	10	8	7	7	98.61	62.91	12.37	2.89	Yes	Segregation
SBP2	30	16	5	5	6	2	75	43.69	20.01	1.56	No	Random
SBP3	27	11	1	0	10	1	—	—	—	—	—	Total dominance
WF	472	103	—	—	—	6	5597.13	6120.82	222.6	−2.35	Yes	Aggregation
WF26	26	42	—	—	—	17	10.93	14.25	0.41	−5.16	Yes	Aggregation

of *P*-values was applied to counteract the increased risk of obtaining false positives.

Ant species identification

Species identifications were based on reference collections at the Biology Centre of the Czech Academy of Sciences, the Australian National Insect Collections (CSIRO), the Harvard Museum of Natural History, online image databases (Antwiki.org, www.antweb.org; www.newguineants.org) and the assistance of taxonomists (see Acknowledgements). With few exceptions, all ant species were barcoded for COI sequences (available in www.formicidaebol.org under field sample codes starting with HP, or PKEE and 4 digits). Vouchers specimens were deposited at the Institute of Entomology, Biology Centre of the Czech Academy of Sciences and the Royal Belgian Institute of Natural Sciences (see species codes in Table S2).

Results

Representativeness of the baitline protocol in terms of arboreal species richness in relation to species dominance

The 31, 30, and 27 canopy trees in plots SBP1, SBP2, and SBP3 sheltered decreasing numbers of ant species (25, 16, 11 species collected, respectively; Fig. 2a,b; Table 2).

In plot SBP1, six species were dominant (Fig. 2a,b), and were represented by two colonies of *Oecophylla smaragdina* (Fabricius 1775) (0.26), one colony of *Anonychomyrma cf. scrutator* (0.19), and one colony of *Crematogaster cf. irritabilis* (0.10). Intraspecific aggressiveness tests could not be conducted for the other dominant species due to limited time in the field: *Podomyrma laevifrons* Smith, F. 1859 (0.23), *Crematogaster meijerei* Emery 1911 (Smith F 1860) (0.13), and *Colobopsis vitrea* (Smith, F. 1860) (0.13).

In plot SBP2, two ant species were territorial and spread over all the trees: *Crematogaster polita* Smith, F. 1865 (0.60, 1 colony) and *O. smaragdina* (0.36, 2 colonies) (Fig. 3a,b).

In plot SBP3, a single territorial species, *Cr. polita*, was found occupying 26 of the 27 trees (species frequency: 0.96) without any intraspecific aggressiveness between workers collected from these trees (Fig. 3c,d).

Non-dominant arboreal ants (i.e., species found above 2 m on trees and not abundant at the baits, category 2, Table 1) were only found in plots SBP1 (eight species, Fig. 2c,d) and SBP2 (five species, Fig. S4a,b) along with seven and six species found only near the ground (category 3), respectively (Fig. 2e,f and Fig. S4c,d). In plot SBP3, dominated by a single colony of *Cr. polita* (0.96), all 10 other ant species belonged to ground-dwelling ants (Fig. S4e,f).

The reference plot WF26, containing 26 canopy trees, hosted 42 ant species. Thus, the SBP1-3 plots underestimated the expected ant species richness as, when the numbers of trees were normalised to 26, the numbers of ant species collected were 22.8, 14.9, and 10.8, something corresponding to only 54.3%, 35.5%, and 25.7% of the WF26 richness (Fig. 4).

Direct versus indirect approaches to detecting territorial ants and ant mosaics

Direct approaches: Aggressiveness tests, co-occurrences at baits, and spatial segregation. Confirmed through aggressiveness tests, we identified four territorial species across the SBP1-3 plots, namely *Cr. polita*, *Cr.* cf. *irritabilis*, *A.* cf. *scrutator*, and *O. smaragdina* (see connections in Figs. 1 and 2). Indeed, when *Cr. polita* and *O. smaragdina* occasionally co-occurred on trees they were vertically segregated (Fig. 3a,b trees #6, 15, 17, 23, and 25). Also, *A.* cf. *scrutator* was vertically segregated from *Cr. polita* (Fig. 3a,b; tree #10).

Field observations revealed co-occurrences on baits between territorial ants and other species (Table S1), illustrating tolerance between *Cr. polita* and *C. vitrea* ($n = 2$ observations). Both were also tolerant of *Pheidole cf. distincta* Donisthorpe, 1943, whereas *Polyrhachis sericata* (Guérin-Méneville, 1838) was tolerated by *Cr. polita* and *A.* cf. *scrutator*, two mutually exclusive territorial ants. Other cases of inter-specific tolerance at the baits are listed in Table S1.

The spatial patterns of territorial ants in the WF plot show the numerical dominance of *Cr. polita*, *A.* cf. *scrutator*, and *C. vitrea* (Fig. 5) that, together, occupied 49.8% of the trees. Nests of *Cr. polita* and *C. vitrea*, noted on 17.6% and 14.0% of the trees, respectively, shared 5.3% of the trees (Fig. 5a). In contrast, although their foragers co-occurred on 10.0% of the trees, *Cr. polita* and *A.* cf. *scrutator* excluded each other spatially (Fig. 5b). Indeed, *A.* cf. *scrutator* was significantly more present

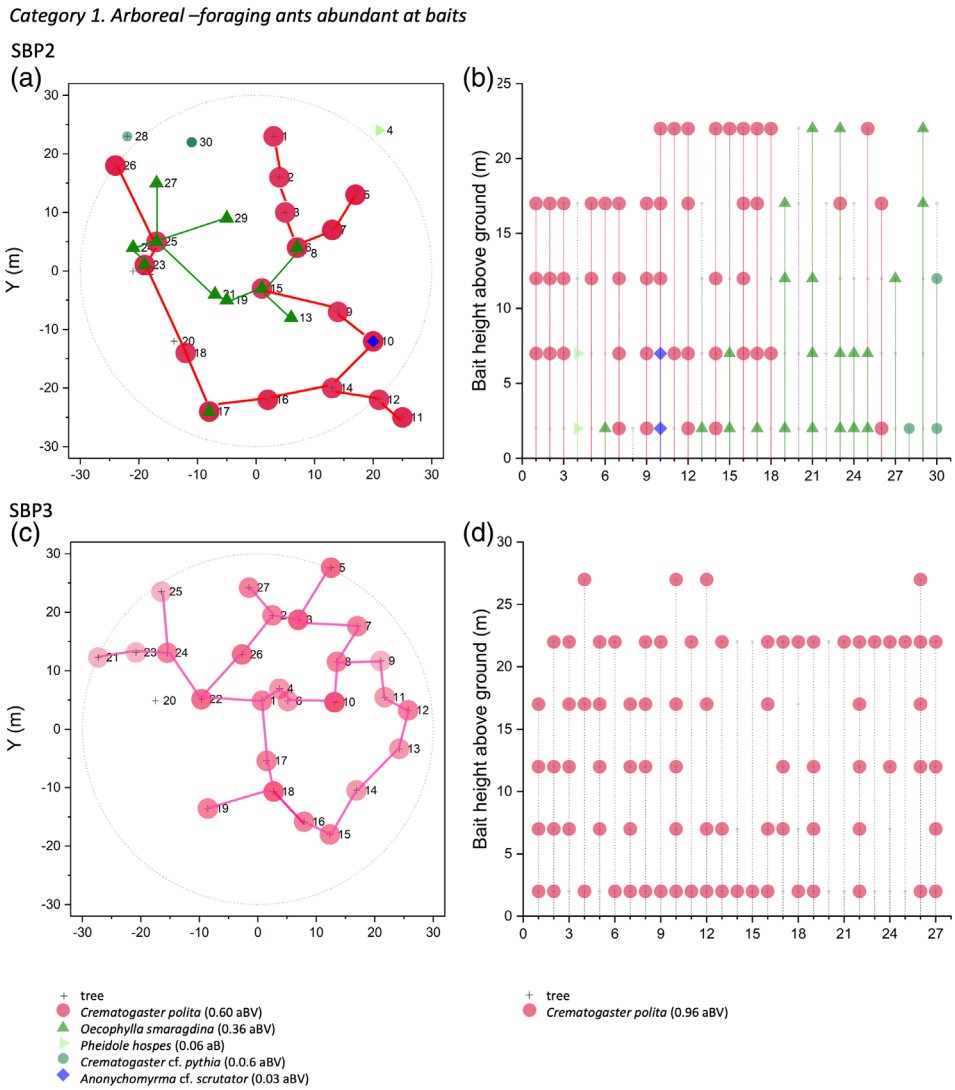

Fig 3. Map of horizontal and vertical species distributions in plots SBP2 (a, b; 30 trees) and SBP3 (c, d; 27 trees). For the sake of brevity, only the arboreal-foraging species, abundant at baits and with a large vertical foraging area in the trees (category 1 in Table 1) are presented. For the other two species categories in plot SBP2, see Fig. S4. Same conventions as in Fig. 2.

on understorey trees than was *Cr. polita* (Mann–Whitney $U = 16645$, $P = 0.022$) and they never nested together (vertical segregation).

Indirect approaches: Null models and sample size. A statistical approach using C-scores resulted in a significant trend towards segregation among the most frequent species in plot SBP1, but without revealing significant pairwise comparisons (Table 2; Fig. 6a). Random patterns were found in SBP2, whether on a global scale or in pairs (Fig. 6b). All trees but one were occupied by a single species in SBP3, so that the C-score analysis was not relevant. In WF26, associations between species pairs were not significant except for an aggregation between *A.* cf. *scrutator* and *Tetraponera laeviceps* (Smith F., 1859) (Fig. 6d).

The importance of the sample size is shown when considering the WF plot (i.e., 472 trees, 103 ant species, including 6 that were frequent) as the higher statistical power revealed more pairwise associations (Table 2; Fig. 6c). Indeed, this time *Cr. polita* appears negatively associated with *A.* cf. *scrutator* and positively associated with two other species including *C. vitrea*. However, compared to the segregation in SBP1, for both WF and WF26 the C-scores suggested a significant aggregation across all the species (Table 2; Fig. 6c,d).

Discussion

Global three-dimensional distribution of arboreal ants

On the basis of the complete survey in the WF plot, we demonstrate here that in Papua New Guinea territorial ants forage on virtually all the ligneous plants in the forest with a clear

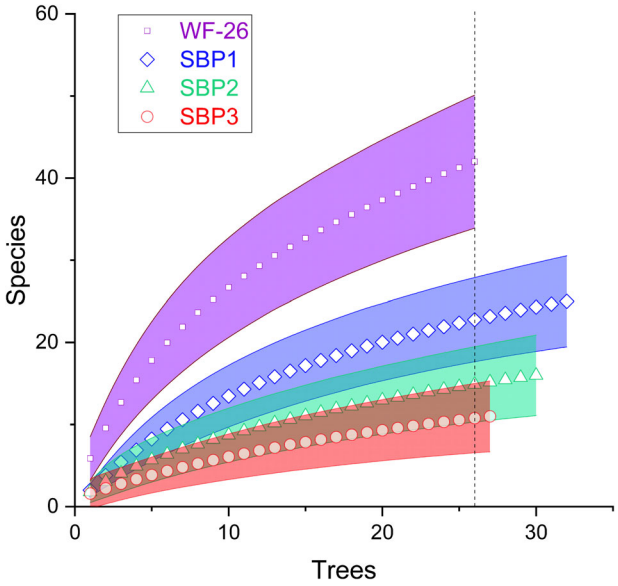

Fig 4. Ant species accumulation in baitline plots SBP1, SBP2, and SBP3, increasingly dominated by a single species, and compared to a baseline census of all arboreal-foraging ants on 26 canopy trees using felling and tree dissection (WF26: dotted line) (Mao-Tau with 95% confidence intervals). All surveys were conducted in lowland primary forests of Papua New Guinea.

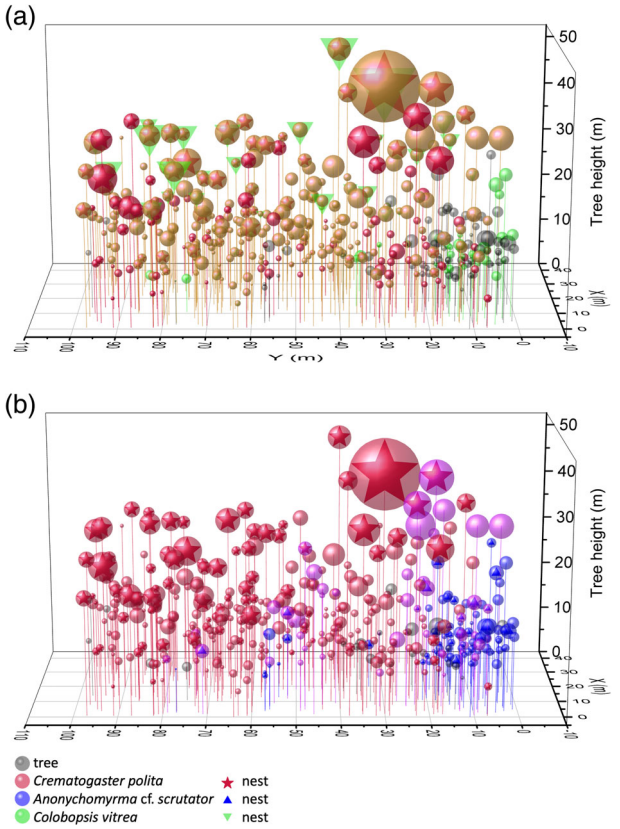

Fig 5. Three-dimensional distribution on trees with a DBH ≥5 cm of the three most frequent arboreal ants in the Whole Forest plot (WF). *Crematogaster polita* (red symbols) was (a) positively associated (aggregated) with the behaviourally subordinate species Colobopsis vitrea (green symbols) but (b) negatively associated (segregated) with *Anonychomyrma cf. scrutator* (blue symbols). Trees occupied by species pairs are shown in mixed colours. Trees without the considered species pair are shown in grey. For greater clarity, symbol sizes are proportional to crown width but are not at the exact scale.

horizontal and vertical spatial segregation between them (Fig. 5). The understorey provides substantial resources for ants in terms of food and/or nesting sites, including for territorial ants such as *A.* cf. *scrutator* (see below) (Klimes, 2017; Orivel *et al.*, 2018; Plowman *et al.*, 2019). In contrast, in Panama, territorial ants were concentrated on the upper parts of trees where resources are the most abundant (Ribeiro *et al.*, 2013). Also, in primary Bornean rainforests numerically dominant species occupy the upper canopy or emergent trees (Yusah *et al.*, 2018); they are absent from lower canopy trees possibly due to a lesser availability of resources (Floren & Linsenmair, 2000).

Intraspecific exclusion from trees

Intraspecific aggressiveness tests revealed that at least four species were territorial: *Cr. polita*, *Cr.* cf. *irritabilis*, *O. smaragdina*, and *A.* cf. *scrutator*. These species possess distinct reproductive and nesting strategies. (i) *C. polita* colonies, remarkable by their ability to dominate the plots studied (Figs. 3 and 5), build a system of large queenright carton nests located in the crowns of large trees and surrounded by numerous small satellite queenless nests located on lower trees (Klimes *et al.*, 2015). Very populous colonies and very aggressive workers allow this species to dominate the Papuan rainforests and plantations, their territories extending over more than 1 ha (Leponce *et al.* (1999). (ii) *Crematogaster cf. irritabilis*, which also builds carton nests, had smaller colonies. (iii) The weaver ant *O. smaragdina* is a well-known territorial ant whose colonies include hundreds of thousands of workers and that builds leaf nests spread over several trees (Hölldobler & Lumsden, 1980). (iv) Finally, *A.* cf. *scrutator* builds its nests inside the branches and trunks of living trees and develops large populations (Klimes, 2017).

All the above-cited species exploit sugary resources from plants or hemipteran trophobionts (Blüthgen & Fiedler, 2002; Klimes, 2017; Plowman *et al.*, 2017; Plowman *et al.*, 2019) enabling them to sustain their huge populations. When tree crowns are not in contact they use interconnecting lianas to pass from one tree to another or form columns on the ground (Adams *et al.*, 2017; Dejean *et al.*, 2019).

Interspecific interactions: Direct versus indirect approaches

Co-occurrences on trees and at the baits indicated a lack of aggressiveness between *C. vitrea* and *Cr. polita*. By contrast, *Cr. polita*, *A.* cf. *scrutator*, and *O. smaragdina* were mutually aggressive.

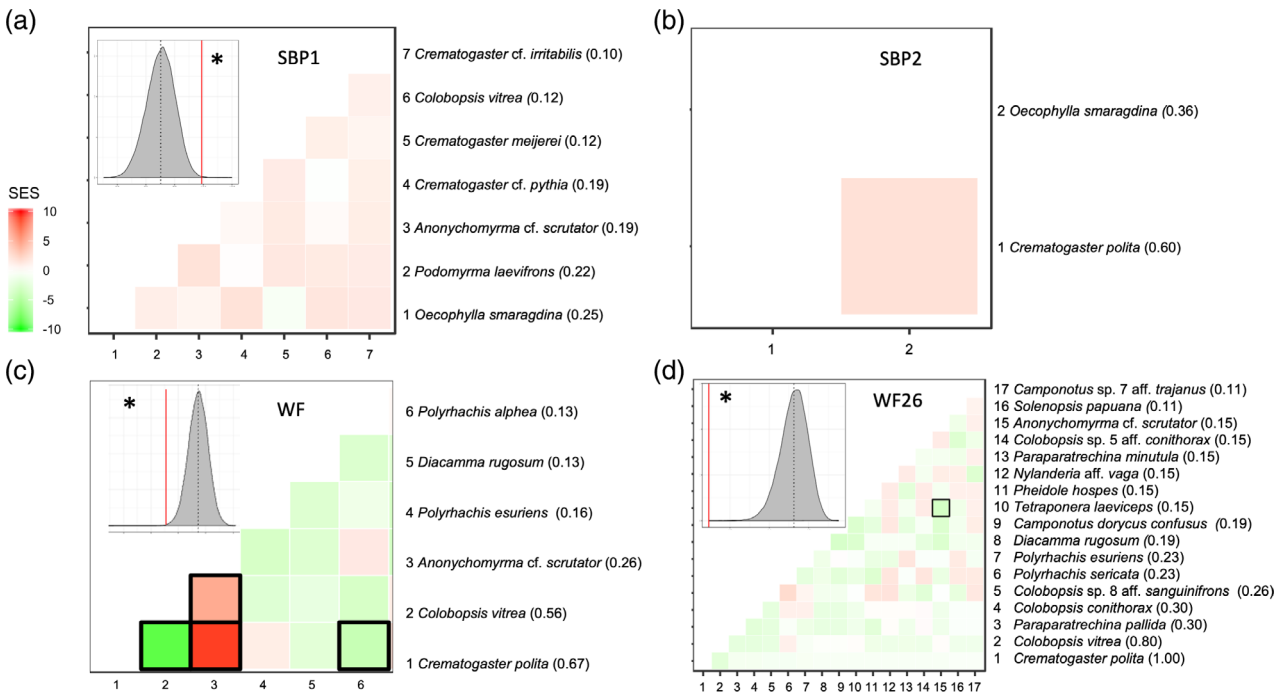

Fig 6. Associations between the most frequent species assessed by C-scores calculated globally and pairwise between individual species for the (a) WF, (b) WF26, (c) SBP1, and (d) SBP2 plots. SES represents a scale of Standardised Effect Sizes of C-scores with higher scores (red) suggesting segregation and lower scores (green) aggregation (positive association) between the species pairs. For pairwise comparisons, the Šidák correction for *P*-values was applied and significant values are delimited by black edges. For global trends (insets in each graph), asterisks indicate that the observed C-score (red vertical line) is significantly different from the randomly assembled community, suggesting segregation, or aggregation within the ant communities in trees (Table 2). The histograms show the frequency of checkerboard units and the dotted lines represent the randomised mean values.

In the large WF dataset, according to the null models, pairwise comparisons were statistically significant for the first three above-mentioned species. Yet, they were below significance in its WF26 subset, illustrating the importance of the sampling size when using this approach, something pointed out by Blüthgen and Stork (2007). The low statistical power associated with small sample sizes was also shown in SBP2 for which a trend towards segregation was found between *Cr. polita* and *O. smaragdina*, but the statistical comparison was not significant.

At the assemblage scale, considering either all or only the most common species, null models are frequently used to prove the existence of ant mosaics when the segregation of species is more frequent than expected by chance. Our results stress that this approach must be used with caution. First, even in plots with a clear spatial segregation between territorial ants (WF, WF26), globally, positive species associations can prevail (Fig. 6c,d). Second, even mutually aggressive territorial ants such as *Cr. polita* and *A. cf. scrutator* (Fig. 4b) or *Cr. polita* and *O. smaragdina* can be found on the same tree, but this does not imply that they are positively or neutrally associated because they can be segregated vertically, as shown through the baitline method (Fig. 3b; see also segregation by sheltering on different main branches of the same crown; Dejean *et al.*, 2007). Third, habitat filtering can result in positive associations (spatial associations). For example *A. cf. scrutator* and *T. laeviceps* nest preferably in smaller trees and living branches (Fig. 5b) (Klimes, 2017). This needs to be distinguished from true behavioural associations such as parabiosis (Menzel & Blüthgen, 2010). For instance, *C. vitrea* and *Cr. polita* co-occurred more than expected by chance in the WF plot (Figs. 5a and 6c) and were even observed twice foraging peacefully on the same bait (Table S1). Cases of tolerance by territorial ants, such as those shown in Table S1, might be due to the production of chemical cues that reduce aggressiveness (Menzel *et al.*, 2013; Birer *et al.*, 2020) and/or differences in body size (Fayle *et al.*, 2015).

In summary, we encountered the full range of interactions between species (i.e., negative, positive, neutral) in all plots studied, which conforms to the definition of 'ant mosaic', but this could not always be detected through statistical methods due to insufficient statistical power.

Conclusion: Pros and cons of the baitline protocol

Compared to previous sampling methods, the baitline method has several advantages. (i) It is the cheapest and quickest method to collect dominant arboreal ants. It is not necessary to have a large infrastructure or expensive equipment such as for canopy cranes, tree felling or fogging. Compared to insecticide fogging, it makes it possible to collect a limited number of individuals to

be identified, and a tree is sampled more quickly than by climbing. While a full census of a felling plot takes nearly a year and several years to sort the ants, a standardised baitline plot requires only 3 days of field work and a similar amount of time to identify the species. (ii) It is safe: it avoids the safety issues associated with climbing, cranes, fogging, and felling (but requires caution when manipulating the sling shot). (iii) It can be used anywhere: unlike climbing (impossible in fragile trees), fogging (often forbidden in protected areas), cranes, and felling (fixed). In addition, unlike fogging, it does not require very light wind conditions to be implemented. (iv) It allows targeted and localised ant sampling: unlike fogging, it is very localised and only collects ants. It is thus possible to obtain a snapshot of the spatial distribution of ants in the tree, particularly of dominant ants. (v) It is non-destructive unlike fogging or felling trees. Live ants can be caught from the ground, unlike with climbing or using a crane, and observations can be repeated. It provides a quantifiable snapshot of where ants are actively foraging vertically on a tree. Behavioural assays between groups of collected specimens provide indications on the 3D extension of the colonies. It solves the problem, often encountered with previous sampling methods, highly demanding in time and resources, of low statistical power for detecting species interactions. (vi) It is very adaptable to the research question. All elements of the baitline method can be modified, including the types of bait, the time spent in the trees, the time of day (e.g., study of nocturnal species), the distance between baits, the number of lines per tree (study of the horizontal distribution of species in the crowns of trees), and the size and shape of the plot.

The limits of the method and the solutions to counter them are the following. (i) Only the fraction of the ant assemblage attracted by baits is sampled. While some species positively or neutrally associated with dominants can be detected (e.g., *C. vitrea*, *Ph. cf. distincta*), many subordinate species might be overlooked (especially when a dominant species monopolises most baits). To obtain precise information on arboreal ant species richness, complementary methods are needed such as arboreal pitfall traps installed along tree trunks (Garcia-Martinez *et al*., 2018; Delabie *et al*., 2020; Law & Parr, 2020; Leponce *et al*., 2021). (ii) The use of exceptionally high quality, patchy baits likely affect ant behaviour through the ants' opportunistic presence and abundance. For example, large amounts of food may saturate small colonies that, attracted to the closest food source, do not forage further, providing an unrepresentative image of the extent of their foraging area. This problem might be corrected by reducing the quantity and quality of food provided and by decreasing the distance between baits. (iii) Except for species building conspicuous large carton nests, it is not possible to define whether or not the collected ants nest in the tree sampled, but a very high abundance at the baits may be an indication of the presence of a nest. (iv) The results of the aggressiveness tests do not provide a definitive answer concerning territorial extension because some dominant species show low levels of intraspecific aggressiveness (e.g., *P. laevifrons*) (Mottl, 2019). In this case, more thorough bioassays or microsatellite markers are required. Nevertheless, previous studies showed that the results of simple aggressiveness tests reflect relatively well genetic variation between arboreal territories at smaller (neighbouring) distances (Frizzi *et al*., 2015). (v) For the statistical analyses of species spatial co-occurrence it is advisable to replicate the protocol or to increase the plot size. This is not difficult since three standardised 0.28 ha plots (i.e., between 80 and 90 canopy trees) can be sampled in 10 days or less by four people. (vi) In Papua New Guinea, ants are more active during the daytime (Novotny *et al*., 1999), but for a more complete understanding of the dynamics of the ant mosaic, it is also recommended to use baitlines at night to verify whether some species are not segregated temporally (Yusah *et al*., 2018).

Our species coding system (Table 1) allows for a quick comparison of ant abundance and distribution between plots and generates more readable maps according to the ant species category (i.e., dominant arboreal, non-dominant arboreal, ground-dwelling; Table 1 and Table S2). This categorisation approach is an attempt to objectively define species dominance even in unknown ant assemblages.

Ants are useful for conservation monitoring (Underwood & Fisher, 2006) but, despite their ecological importance, canopy ants have not been used so far due to the difficulty of collecting them. The baitline method overcomes this obstacle and offers the possibility of monitoring population trends of ecologically dominant species or of invasive species.

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DATA AVAILABILITY STATEMENT

The data, Rcode, and video that support the findings are openly available at DOI:10.5281/zenodo.4554164

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting information.

Video S1: The successive steps of the standardised baitline protocol. Video shot in Papua New Guinea (2012), in collaboration with Bonny Koane and the local communities of Mt. Wilhelm. For explanations, see Fig.1 (format HD, 16:9, 3′48″).

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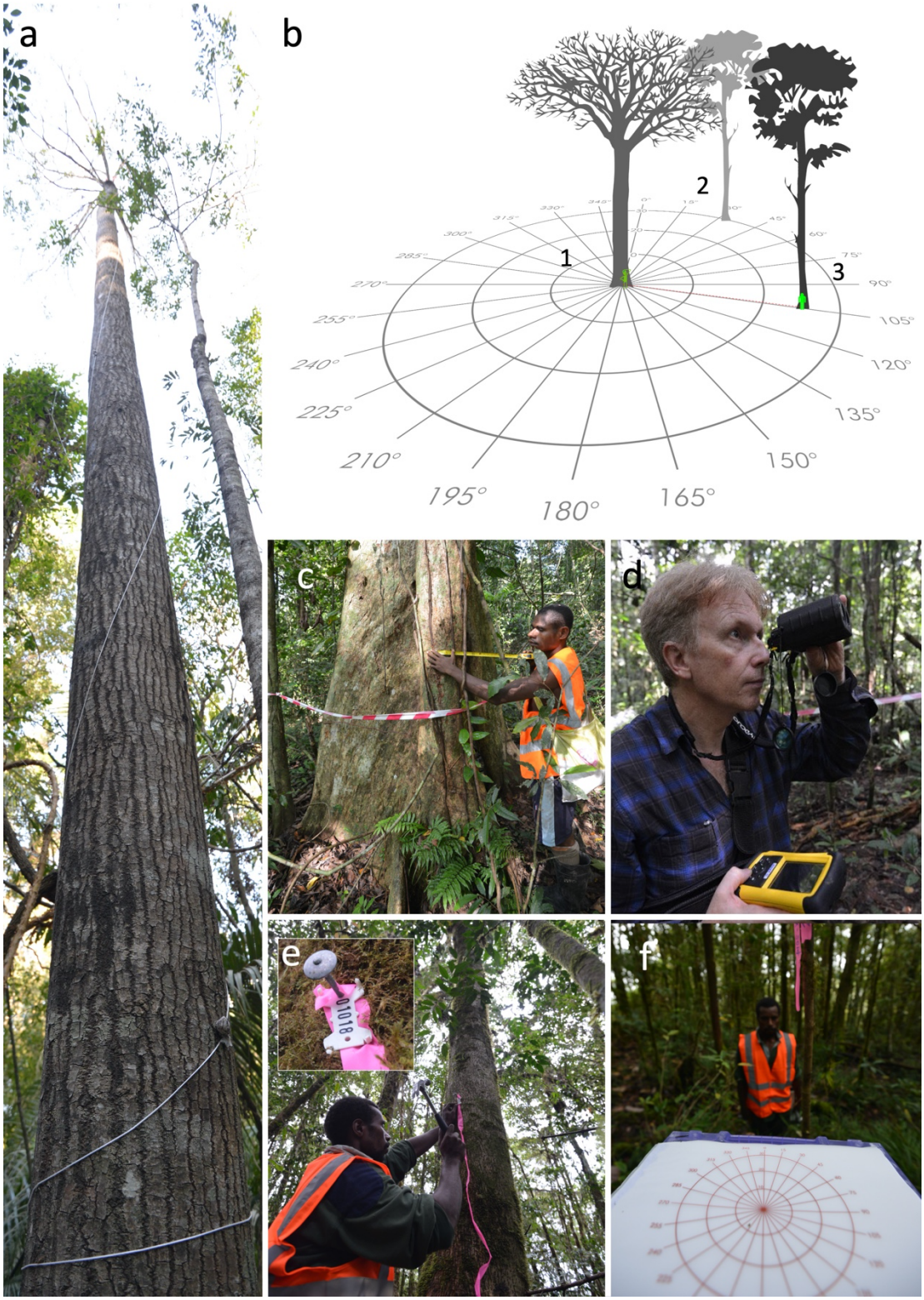

Fig. S1. Plot & tree marking: (a) A tall tree (emergent) is used as a landmark to position the centre of the plot. Please note that it is shown here with baitlines already installed. (b) Around the central tree (labelled #1), all the trees forming the upper canopy (exposed to direct sunlight) are selected within a 30m radius. The trees are mapped and numbered clockwise according to

the increasing angle (North = 0°) and distance from the central tree. (c) Flagging tape put around the central tree trunk and hanging from a high branch allow it to be seen from far away (d) A compass and rangefinder are used to number the map, the location and height of the trees. (e) The trees are tagged and flagged. (f) The vertical flag is facing the central tree (allowing the centre of the plot to be found again easily).

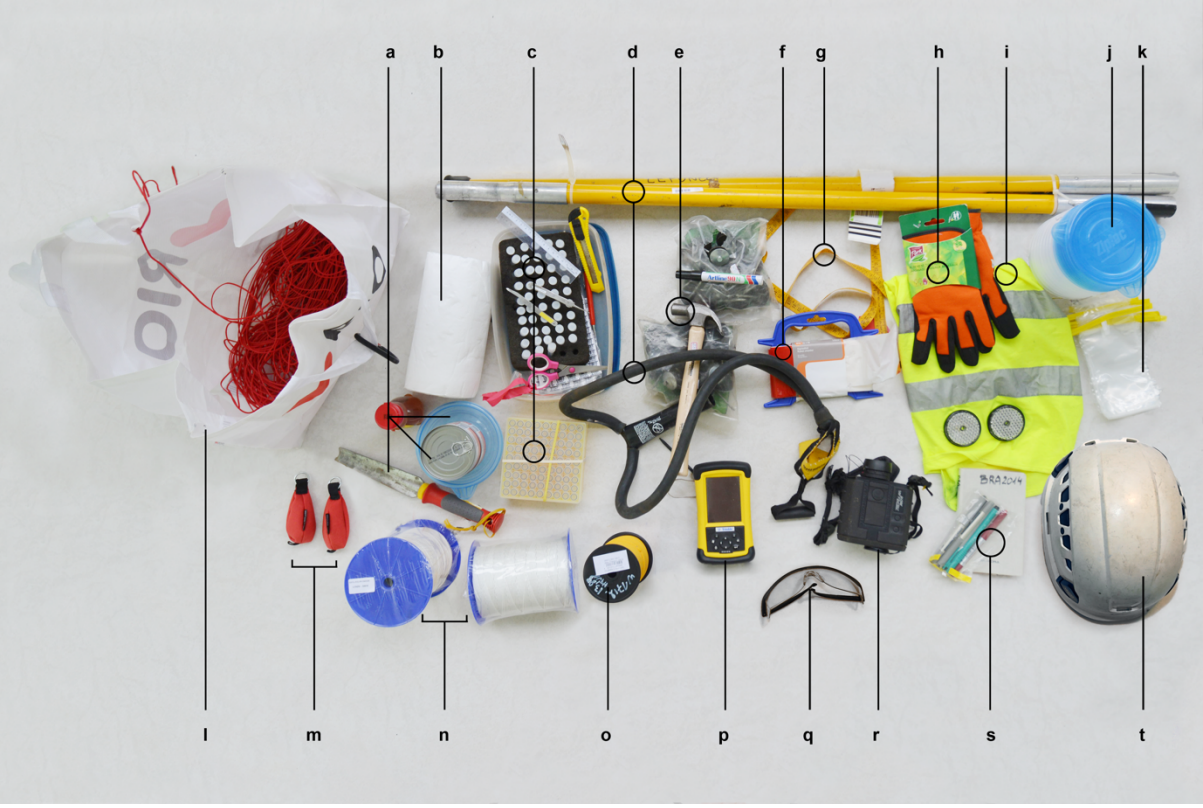

Fig. S2. Overview of the equipment and consumables needed for the standardised baitline protocol: (a) weeding knife used as a spoon to prepare baits (5 tins of tuna in natural oil per plot + tin opener); (b) paper towel used for baits and during aggressiveness tests (rolls usually have around 50 sheets allowing 100 baits to be prepared) and honey (<100 g per plot); (c) vials, labels, scissors, forceps to collect voucher specimens; (d) sling shot to throw arborist lines into trees (e.g., Sherill Tree® Big Shot, FTC® Sling-line 3); (e) hammer, nails and marker to tag trees; (f) flagging tape; (g) measuring tape to measure tree diameter; (h) gloves used as hand protection when shooting; (i) safety vest with bands reflecting the laser beam of the

rangefinder; (j) containers used during aggressiveness tests between colonies (e.g. urine pots); (k) whirl-paks as multi-use containers; (l) arborist throw line, which does not tangle, stored in a bag; (m) throw bags; (n) UV-resistant polyamide 1.5mm lines along which baits are installed; (o) 50m spare throw line; (p) rugged handheld computer to note the observations; (q) safety glasses; (r) laser rangefinger with clinometer and compass for mapping trees and measuring their height (e.g., TruPulse® 360R); (s) notebook and water resistant pen; and (t) helmet used as head protection when shooting throw bags.

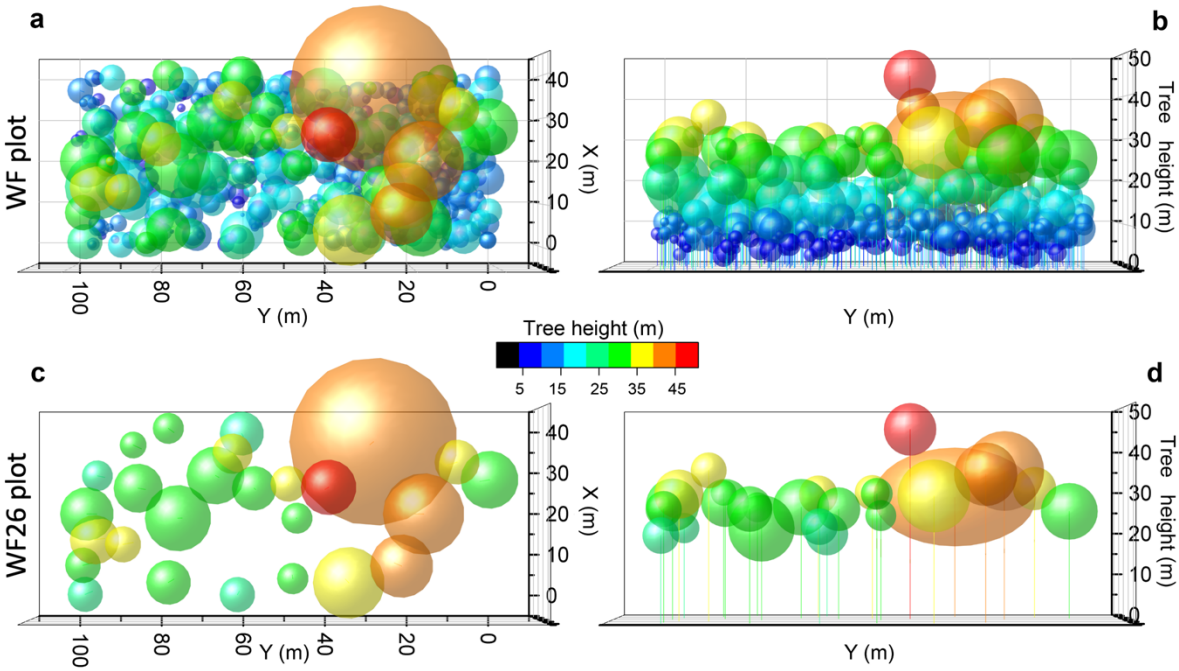

Fig. S3. Tree crowns, mapped from above (left) and laterally (right), (a, b) of all trees with DBH ≥ 5cm in the Whole Forest plot ("WF" dataset, 472 trees) and (c, d) the subset of the tallest canopy trees ("WF26" dataset, 26 trees). Bubbles represent the maximum crown diameter. Tree crowns are coloured according to the maximum height of the tree. Emergent trees (red bubbles) and upper canopy trees (orange, yellow, green) are exposed to direct sunlight. They are targeted by the Standardized Baitline protocol. They shade subcanopy (turquoise) and understorey (blue) trees.

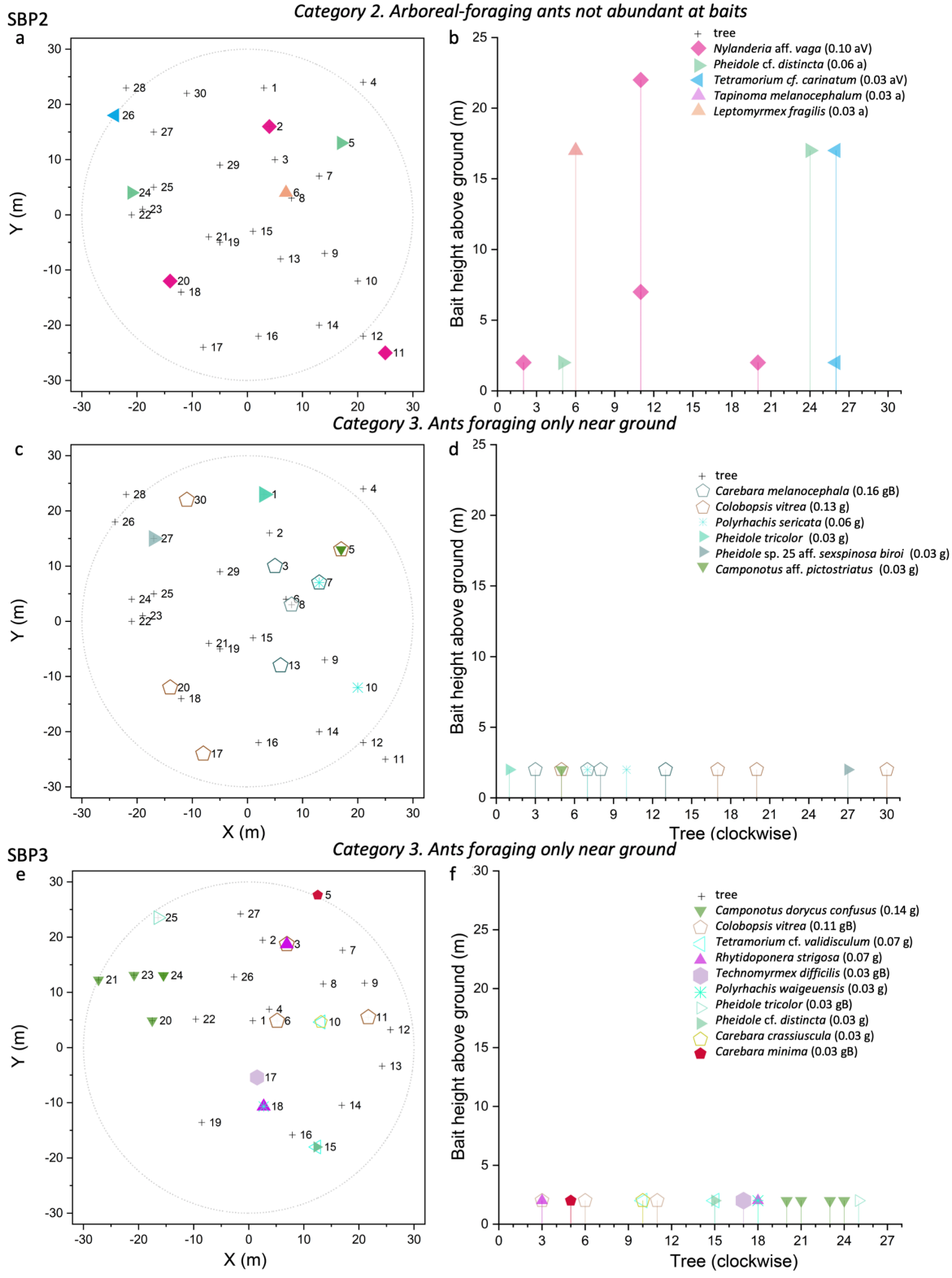

Fig. S4. Complement to Fig.3 (distribution of arboreal-foraging ants dominant at the baits, category 1, see Table 1) showing the distribution of arboreal-foraging ants not dominant at

the baits (category 2) and ants foraging only near the ground (category 3) in plots SBP2 and SBP3. There were no ground-nesting ants in SBP3. Conventions as in Fig. 2 and 3.

Appendix 1.

Video shot in Papua New Guinea (2012), in collaboration with Bonny Koane and the local communities of Mt. Wilhelm. For explanations, see Fig.1 (format HD, 16:9, 3'48").

Appendix 2. Standardised Baitline Protocol: typical timing (1 supervisor, 1 assistant trained in slingshot handling and two other assistants)

The supervisor is experienced in the technique. The helpers can be villagers trained on site. Two groups are formed: one dedicated to marking, baiting and collecting ("baiters") and the other to installing/removing the lines ("shooters").

Day 1

- Search for an appropriate study site (e.g., undisturbed) that appears representative of the area and with a tall tree in the centre.
- The team leader trains the shooter in the use of the slingshot. A safety briefing is given at the same time to all team members.

- Group 1: Marks all trees constituting the canopy within 30 m of the plot (Fig. S1 -step 1) (about 4 hours for 30 trees).
- Group 2: Installs the ropes in the trees tagged by group 1 (Fig. S1 -step 2).

Day 2

- Group 1 – morning: prepares and installs the baits in the trees (Fig. S1 -step 2)
- Group 1 – afternoon: collection of ants with baits, mapping of their distribution, beginning of aggressiveness tests (Fig. S1 -steps 3 & 4). Baits are put back into the trees to obtain fresh ants for the aggressiveness tests on the next day.
- Group 2: continues and completes the installation of the ropes. Helps group 1 when finished.

Day 3

- Group 1 – morning: prepares and installs the baits in the trees (Fig. S1 -step 2)
- Group 1 – afternoon: collection of ants with baits, mapping of their distribution, continuation of aggressiveness tests (Fig. S1 -steps 3 & 4)

Group 2 helps group 1 and removes all ropes at the end of the day

Table S1. Field observations of species' mutual tolerance on the baits in plots SBP1, SBP2 and SBP3. The values in cells represent the number of specimens observed on baits (usually estimated when over 10 individuals).

Plot - #Tree - Bait height	**SBP1 #22-17m**	**SBP1 #27-17m**	**SBP1 #30-17m**	**SBP1 #4-2m**	**SBP1 #11-2m**	**SBP2 #2-2m**	**SBP2 #4-2m**	**SBP2 #6-7m**	**SBP2 #6-22m**	**SBP2 #10-2m**	**SBP2 #17-2m**	**SBP2 #19-2m**	**SBP2 #28-2m**	**SBP2 #30-2m**	**SBP2 #30-17m**	**SBP3 #6-2m**	**SBP3 #11-2m**	**SBP3 #16-2m**
Species name																		
***Anonychomyrma cf. scrutator* (Smith F., 1859)**							50											
***Anonychomyrma minuta* (Donisthorpe, 1943)**			20															
***Colobopsis vitrea* (Smith F., 1860)**				1														
***Colobopsis vitrea* (Smith F., 1860)**						5					2	3	1					
***Colobopsis vitrea* (Smith F., 1860)**																6	20	
***Camponotus wanangus* Klimes & McArthur, 2014**			50															
***Camponotus (Myrmamblys) aff. pictostriatus* Karavaiev, 1933**						1												
***Carebara melanocephala* Donisthorpe, 1948**										50								
***Crematogaster polita* Smith F., 1865**								20	20	10				6	50			
***Crematogaster polita* Smith F., 1865**																50	50	50
***Crematogaster cf. pythia* Forel, 1915**				10	10													
***Crematogaster cf. pythia* Forel, 1915**													9					
***Crematogaster meijerei* Emery, 1911**		20																
***Oecophylla smaragdina* (Fabricius, 1775)**		10																
***Oecophylla smaragdina* (Fabricius, 1775)**											10							
***Nylanderia aff. vaga* (Forel, 1901)**					5													
***Nylanderia aff. vaga* (Forel, 1901)**								2	2			2						
***Pheidole cf. distincta* Donisthorpe, 1943**						5												
***Pheidole cf. distincta* Donisthorpe, 1943**																		1
***Podomyrma laevifrons* Smith F., 1859**	20																	
***Polyrhachis (Myrma) sericata* (Guérin-Méneville, 1838) (relucens-group)**							1			1								
***Polyrhachis (Myrmhopla) waigeuensis* Donisthorpe, 1943 (sexspinosa-group)**					10													
***Tetramorium cf. carinatum* (Smith F., 1859)**														10	2			
***Turneria dahlii* Forel, 1901**	1																	
Number of co-occurring species on the bait	**2**	**2**	**2**	**2**	**3**	**3**	**2**	**2**	**2**	**3**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**

Table S2. List of species collected in the Standardised Baitline Protocol (SBP) plots and in the Whole Forest (WF) plot. All plots were established in lowland primary forests located within a range of 82 km. The coding system for the frequency of the species in the plots, their foraging strata, numerical dominance at the baits, and vertical distribution on the trees follows the convention presented in Table 1. Species codes (SpCode_PK) are consistent with previous publications by P. Klimes.

	SpCode_PK	Species	SubFamily	SBP1	SBP2	SBP3	WF	WF26
1	ANOC001	*Anochetus cato* Forel, 1901	Ponerinae				0.002	
2	ANON001	*Anonychomyrma cf. scrutator* (Smith F., 1859)	Dolichoderinae	0.19 aBV	0.03 aBV		0.261	0.15
3	ANON002	*Anonychomyrma minuta* (Donisthorpe, 1943)	Dolichoderinae	0.03 aB			0.017	0.04
4	APHA001	*Aphaenogaster sp. aff. dromedaria* (Emery, 1900)	Myrmicinae				0.002	
5	BOTH001	*Chronoxenus rossi Donisthorpe,* 1950	Dolichoderinae				0.002	
6	CAMP001	*Colobopsis vitrea* (Smith F., 1860)	Formicinae	0.12 aBV	0.13 g	0.11 gB	0.561	0.81
7	CAMP003	*Camponotus wanangus* Klimes & McArthur, 2014	Formicinae	0.06 aBV			0.023	0.08
8	CAMP004	*Colobopsis aruensis* Karavaiev, 1933	Formicinae				0.006	
9	CAMP005	*Colobopsis sp. 5 aff. conithorax* Emery, 1914	Formicinae				0.100	0.15
10	CAMP006	*Colobopsis conithorax* Emery, 1914	Formicinae				0.085	0.31
11	CAMP007	*Camponotus (Myrmamblys) sp. 7 aff. trajanus* Forel, 1912	Formicinae				0.044	0.12
12	CAMP008	*Colobopsis sp. 8 aff. sanguinifrons* Viehmeyer, 1925	Formicinae				0.078	0.27
13	CAMP010	*Colobopsis cf. macrocephala* (Erichson, 1842)	Formicinae				0.008	
14	CAMP011	*Camponotus (Myrmamblys) aff. pictostriatus* Karavaiev, 1933	Formicinae		0.03 g		0.013	0.04
15	CAMP013	*Colobopsis quadriceps* (Smith F., 1859)	Formicinae				0.002	
16	CAMP014	*Colobopsis rotunda* Klimes & McArthur, 2014	Formicinae				0.004	
17	CAMP016	*Camponotus (Tanaemyrmex) dorycus confusus* Emery, 1887	Formicinae			0.14 g	0.019	0.19
18	CAMP017	*Colobopsis aff. polynesica* (Emery, 1896)	Formicinae				0.002	0.04
19	CAMP018	*Camponotus (Tanaemyrmex) cf. variegatus* (Smith, F., 1858)	Formicinae				0.004	
20	CAMP019	*Camponotus triangulatus* Klimes & McArthur, 2014	Formicinae				0.019	
21	CAMP020	*Camponotus (Myrmamblys) sp. 20 aff. janeti* Forel, 1895	Formicinae				0.008	
22	CAMP022	*Camponotus anezkae* Klimes & McArthur, 2014	Formicinae				0.008	

23	CARE001	*Carebara minima* (Emery, 1900)	Myrmicinae			0.03 gB		
24	CARE002	*Carebara atoma* Emery, 1900	Myrmicinae				0.002	
25	CARE006	*Carebara crassiuscula* (Emery, 1900)	Myrmicinae	0.03 gB		0.03 g		
26	CARE007	*Carebara melanocephala* Donisthorpe, 1948	Myrmicinae		0.16 gB			
27	CERA001	*Cerapachys cf. flavaclavatus* Donisthorpe, 1938	Dorylinae				0.002	
28	CERA002	*Cerapachys desposyne* Wilson, 1959	Dorylinae				0.002	
29	CREM002	*Crematogaster elysii* Mann, 1919	Myrmicinae				0.093	
30	CREM003	*Crematogaster polita* Smith F., 1865	Myrmicinae		0.60 aBV	0.96 aBV	0.667	1
31	CREM004	*Crematogaster cf. pythia* Forel, 1915	Myrmicinae	0.19 a	0.06 aBV		0.015	
32	CREM005	*Crematogaster flavitarsis* Emery, 1900	Myrmicinae	0.06 aBV				
33	CREM006	*Crematogaster sp. 6*	Myrmicinae	0.03 g			0.006	
34	CREM007	*Crematogaster sp. 7 aff. fritzi* Emery, 1901	Myrmicinae				0.087	0.04
35	CREM011	*Crematogaster sp. 11 aff. fritzi* Emery, 1901	Myrmicinae				0.006	0.04
36	CREM014	*Crematogaster cf. irritabilis* Smith, F., 1860	Myrmicinae	0.10 aBV			0.036	0.04
37	CREM020	*Crematogaster meijerei* Emery, 1911	Myrmicinae	0.12 aBV				
38	DIAC001	*Diacamma rugosum* (Le Guillou, 1842)	Ponerinae				0.127	0.19
39	ECHI001	*Echinopla sp. 1 aff. australis* Emery, 1897	Formicinae				0.008	
40	ECHI002	*Echinopla* sp. 2	Formicinae				0.004	
41	HYPO002	*Hypoponera cf. confinis* Roger, 1860	Ponerinae				0.006	0.04
42	HYPO003	*Hypoponera sabrone* Donisthorpe, 1941	Ponerinae				0.002	
43	LEPM001	*Leptomyrmex fragilis* (Smith F., 1859)	Dolichoderinae		0.03 a		0.008	0.04
44	LORD001	*Lordomyrma sp. 1*	Myrmicinae				0.002	
45	MONO003	*Monomorium sp. 3*	Myrmicinae	0.06 aV			0.004	0.04
46	MONO004	*Monomorium pharaonis* (Linnaeus 1758)	Myrmicinae				0.002	
47	ODON001	*Odontomachus simillimus* Smith F., 1858	Ponerinae				0.002	
48	ODON002	*Odontomachus testaceus* Emery, 1897	Ponerinae				0.006	0.04
49	OECO001	*Oecophylla smaragdina* (Fabricius, 1775)	Formicinae	0.25 aBV	0.36 aBV		0.015	0.04
50	PACH006	*Brachyponera croceicornis* (Emery,1900)	Ponerinae				0.002	
51	PARA001	*Paraparatrechina pallida* Donisthorpe, 1947	Formicinae	0.03 a			0.087	0.31
52	PARA002	*Paraparatrechina sp. 2*	Formicinae				0.006	

53	PARA003	*Paraparatrechina minutula* (Forel, 1901)	Formicinae				0.076	0.15
54	PARA005	*Nylanderia aff. vaga* (Forel, 1901)	Formicinae	0.06 g	0.10 aV		0.034	0.15
55	PARA006	*Paraparatrechina sp. 6*	Formicinae				0.002	
56	PARA007	*Nylanderia nuggeti* Donisthorpe, 1941	Formicinae	0.03 a			0.004	
57	PHEI002	*Pheidole sp. 2 aff. sexspinosa biroi* Emery, 1900	Myrmicinae				0.002	
58	PHEI004	*Pheidole hospes* Smith, F. 1865	Myrmicinae	0.03 a	0.06 aB		0.025	0.15
59	PHEI007	*Pheidole sp. 7 aff. gambogia* Donisthorpe, 1948	Myrmicinae				0.011	
60	PHEI013	*Pheidole sp. 13 aff. tricolor*, Donisthorpe, 1949	Myrmicinae				0.002	
61	PHEI014	*Pheidole sp. 14 aff. gambogia* Donisthorpe, 1948	Myrmicinae	0.06 a			0.011	
62	PHEI018	*Pheidole cf. distincta* Donisthorpe, 1943	Myrmicinae	0.06 gB	0.06 a	0.03 g		
63	PHEI024	*Pheidole sp. 24* aff. amber Donisthorpe, 1941	Myrmicinae				0.051	0.04
64	PHEI025	*Pheidole sp. 25* aff. sexspinosa biroi Emery, 1900	Myrmicinae		0.03 g		0.004	0.08
65	PHEI026	*Pheidole sp. 26*	Myrmicinae				0.002	
66	PHEI035	*Pheidole tricolor* Donisthorpe, 1949	Myrmicinae		0.03 g	0.03 gB		
67	PHIL001	*Philidris cf. cordata* (Smith F., 1859)	Dolichoderinae	0.06 aBV			0.015	0.08
68	PHIL002	*Philidris sp. 2 aff. 1*	Dolichoderinae				0.006	
69	PHIL003	*Philidris sp. 3 aff. 1*	Dolichoderinae				0.006	
70	PODO001	*Podomyrma laevifrons* Smith F., 1859	Myrmicinae	0.22 aBV				
71	PODO002	*Podomyrma sp. 2 aff. basalis* Smith F., 1859	Myrmicinae				0.019	0.04
72	PODO003	*Podomyrma sp. 3 aff. laevifrons* Smith F., 1859	Myrmicinae				0.028	
73	POLY001	*Polyrhachis (Myrmhopla) esuriens* Emery, 1897 (sexspinosa-group)	Formicinae				0.163	0.23
74	POLY002	*Polyrhachis (Myrma) sericata* (Guérin-Méneville, 1838) (relucens-group)	Formicinae		0.06 g		0.040	0.23
75	POLY004	*Polyrhachis (Cyrtomyrma) debilis* Emery, 1887	Formicinae				0.068	
76	POLY008	*Polyrhachis (Myrmatopa) alphea* Smith F.,1863 (*flavicornis*-group)	Formicinae				0.108	0.08
77	POLY010	*Polyrhachis (Myrmatopa) luteogaster* Kohout, 2012 (*flavicornis*-group)	Formicinae				0.072	
78	POLY011	Polyrhachis (Myrmothrinax) queenslandica Emery, 1895 (*thrinax*-group)	Formicinae				0.017	
79	POLY014	*Polyrhachis (Myrmatopa) sp. nov.* (*flavicornis*-group)	Formicinae				0.002	

80	POLY015	*Polyrhachis (Myrmhopla) waigeuensis* Donisthorpe, 1943 (sexspinosa-group)	Formicinae	0.09 gB		0.03 g	0.068	0.08
81	POLY016	*Polyrhachis (Myrmhopla) mucronata* Smith F., 1859 (*mucronata*-group)	Formicinae				0.015	
82	POLY019	*Polyrhachis (Myrmatopa) lombokensis* Emery, 1898 (*wallacei*-group)	Formicinae				0.015	
83	POLY020	*Polyrhachis (Myrmatopa) dolomedes* Smith F., 1863 (schang-group)	Formicinae				0.008	
84	POLY021	*Polyrhachis (Aulacomyrma) pallipes* Donisthorpe, 1948 (dohrni-group)	Formicinae				0.006	
85	POLY023	*Polyrhachis (Myrmhopla) sp. nov. aff. bubastes* Smith F., 1863 (sexspinosa-group)	Formicinae				0.002	0.04
86	POLY029	*Polyrhachis (Campomyrma) xiphias* Smith, F. 1863	Formicinae				0.002	
87	PSEU001	*Pseudolasius cf. breviceps* Emery, 1887	Formicinae				0.002	
88	RHYT002	*Rhytidoponera strigosa* (Emery, 1887)	Ectatomminae	0.03 g		0.07 g	0.008	
89	ROGE001	*Rogeria cf. stigmatica* Emery, 1897	Myrmicinae				0.008	0.04
90	SOLE004	*Solenopsis papuana* Emery, 1900	Myrmicinae				0.034	0.12
91	STRU002	*Strumigenys szalayi* Emery, 1897	Myrmicinae				0.006	
92	STRU003	*Strumigenys cf. racabura* Bolton, 2000	Myrmicinae				0.004	
93	TAPI001	*Tapinoma melanocephalum* (Fabricius, 1793)	Dolichoderinae	0.03 g	0.03 a		0.002	0.04
94	TAPI002	*Tapinoma cf. indicum* Forel, 1895	Dolichoderinae				0.006	0.04
95	TAPI003	*Tapinoma sp. 3* aff. williamsi (Wheeler 1935)	Dolichoderinae				0.013	
96	TECH001	*Technomyrmex cf. brunneus* Forel, 1895	Dolichoderinae				0.004	
97	TECH002	*Technomyrmex albipes* (Smith F., 1861)	Dolichoderinae	0.03 a			0.017	
98	TECH003	*Technomyrmex difficilis* Forel 1892	Dolichoderinae			0.03 gB	0.015	0.08
99	TECH004	*Technomyrmex albicoxis* Donisthorpe, 1945	Dolichoderinae				0.002	
100	TECH005	*Technomyrmex gilvus* Donisthorpe, 1941	Dolichoderinae				0.006	
101	TETP001	*Tetraponera laeviceps* (Smith F., 1859)	Pseudomyrmecinae				0.078	0.15
102	TETP002	*Tetraponera nitida* (Smith F., 1860)	Pseudomyrmecinae				0.002	
103	TETP003	*Tetraponera atra* Donisthorpe, 1949	Pseudomyrmecinae				0.004	
104	TETP004	*Tetraponera modesta* (Smith F., 1860)	Pseudomyrmecinae				0.002	
105	TETR002	*Tetramorium kydelphon* Bolton, 1979	Myrmicinae				0.015	0.04
106	TETR003	*Tetramorium cf. validisculum* Emery, 1897	Myrmicinae			0.07 g	0.006	

107	TETR006	*Tetramorium sp. 6 aff. validisculum* Emery, 1897	Myrmicinae				0.021	
108	TETR012	*Tetramorium pulchellum* Emery, 1897	Myrmicinae				0.002	
109	TETR016	*Tetramorium sp. 12 aff. pulchellum* Emery, 1897	Myrmicinae				0.004	0.04
110	TETR017	*Tetramorium cf. carinatum* (Smith F., 1859)	Myrmicinae		0.03 aV			
111	TURN001	*Turneria dahlii* Forel, 1901	Dolichoderinae	0.03 a				
112	TURN002	*Turneria cf. pacifica* Mann, 1919	Dolichoderinae				0.002	
113	VOLL001	*Vollenhovia brachycera* Emery, 1897	Myrmicinae				0.006	