

The University of South Bohemia in České Budějovice

Faculty of Science

**Foraging activity and species composition of ants during day/night
in primary and secondary forests in Papua New Guinea**

Master's thesis

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Annotation

This study examines diel foraging activity and species composition of vertically stratified ant communities between primary and secondary forests in Papua New Guinea. To determine the diel foraging activity and changes in species composition of ants, the abundance was estimated/approximated from baits on tree trunks or the forest floor.

Declaration

I hereby declare that I have worked on my master's thesis independently and used only the sources listed in the bibliography. I hereby declare that, in accordance with Article 47b of Act No. 111/1998 in the valid wording, I agree with the publication of my master's thesis, in full to be kept in the Faculty of Science archive, in electronic form in a publicly accessible part of the IS STAG database operated by the University of South Bohemia in České Budějovice accessible through its web pages. Further, I agree to the electronic publication of the comments of my supervisor and thesis opponents and the record of the proceedings and results of the thesis defense in accordance with Act No. 111/1998. I also agree to the comparison of the text of my thesis with the Theses.cz thesis database operated by the National Registry of University Theses and a plagiarism detection system. České Budějovice, 13 April 2023

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1. Literature review

1.1. Environmental gradients and vertical stratification in tropical rainforests of Papua New Guinea

Papua New Guinea is a tropical region renowned for its unparalleled biodiversity, accounting for 5% of the world's species richness. As one of the five designated high biodiversity wilderness areas, it is considered a global biodiversity hotspot with 20,000 species of vascular plants (Swartzendruber, 1993). The region's dense rainforests encompass a diverse range of forest habitats shaped by the climatic zones influenced by the presence of mountain ranges of recent geological origin (Toussaint et al., 2014).

Tropical rainforests, including those in Papua New Guinea, are characterised by a high degree of complexity and variability, resulting from the interplay of multiple ecological processes and their response to varying environmental gradients (Paijmans, 1976). One of the significant gradients is the vertical gradient, formed by the arrangement of trees, specifically by canopy height and complexity (Ozanne et al., 2003; Klinges & Scheffers, 2020; Sagar & Devy, 2022). This results in a steep variation of resources and environmental conditions within the tropical rainforests (Ozanne et al., 2003; De Frenne et al., 2019).

The vegetation of the forest canopies serves as an environmental modulator, mitigating the effects of solar radiation on the lower strata of the forest, resulting in a more stable, cooler, and humid climate in contrast with the upper layers (De Frenne et al., 2019). This results in environmental gradients that can be many orders of magnitude higher than those driven by latitude or altitude (Scheffers et al., 2013, 2014). For instance, in the tropical rainforests of the Philippines, the temperature changes by 2.2 °C within a 20 m of vertical layer, while only showing a difference of 0.7 °C per 100 m increase in altitude (Scheffers et al., 2013). The variations in relative humidity, wind speed, ultraviolet radiation, and light are also significant. The relative humidity gradient can account for up to 10% of the difference between the tree canopy and the forest floor in favour of the lower strata (Scheffers et al., 2013, 2014). In contrast, wind speed, ultraviolet radiation, and gradient of light reach their highest values at the top of the forest canopy (McCay, 2003; Ozanne et al., 2003; Law et al., 2020). In addition, the aboveground portion of the tree consists of diverse microhabitats such as tree openings, epiphytes, and tree ferns increasing habitat heterogeneity and providing thermal refugia for

different taxa (Barthlott et al., 2001; Woods, 2013; De Frenne et al., 2019; Sagar & Devy, 2022).

However, canopy height and complexity can display substantial differences between primary and secondary forests (Ewers & Banks-Leite, 2013; Sagar & Devy, 2022). Specifically, secondary forests, with their lower canopy height and reduced complexity, are more susceptible to extreme environmental conditions in comparison to the taller and more complex canopies found in primary forests (Barthlott et al., 2001; Ewers & Banks-Leite, 2013; De Frenne et al., 2019; Sagar & Devy, 2022). Despite the differences between the different forest types, the tropical rainforest's three-dimensional structure, with its environmental conditions, contributes to niche diversification and creates a microgeographical pattern of species distribution, known as vertical stratification (Oliveira & Scheffers, 2019).

Vertical stratification of species in tropical rainforests is a product of natural selection that shapes the physiological and behavioural adaptations of species (Kaspari et al., 2015; Bujan et al., 2016). These traits, in conjunction with the influence of environmental conditions, determine the species' fundamental vertical niche (Leahy et al., 2020). The realisation of this niche is further influenced by the distribution of resources, the presence of natural enemies, competition and limitations on dispersal, leading to variations in the abundance, richness, and biotic interactions among species across vertical forest strata (Basset, 2001; Loiselle & Farji-Brener, 2002; Van Bael et al., 2003; Dial et al., 2006; Chmel et al., 2016).

Furthermore, tropical rainforest climatic conditions exhibit diurnal and seasonal fluctuations, marked by shifts in precipitation, temperature, and humidity over diurnal and seasonal scales (Park, 2003). These shifts in climate create an additional environmental gradient that, through physiological constraints, results in the partitioning of species not just space but also in time (Lee et al., 2014; Basham & Scheffers, 2020; Kuchenbecker et al., 2021). Additionally, temporal changes in environmental conditions can have a significant impact on the trophic networks in tropical ecosystems (Lee et al., 2014; Molleman et al., 2016; Anjos et al., 2017; Kuchenbecker et al., 2021). For instance, shifts in temperature and humidity can cause an increase in the activity and abundance of primary consumers through the alteration of plant phenology (Lee et al., 2014; Anjos et al., 2017; Kuchenbecker et al., 2021). Consequently, these shifts in populations of primary consumers can lead to alterations in predator-prey interactions (Schöning et al., 2008; Molleman et al., 2016).

Given the large variability of environmental conditions, the temporal fluctuations have a greater impact on the tree canopy, which is exposed to fluctuations of temperatures and more

harsh conditions, in contrast to the more stable and protected understory of tropical rainforests. This can result in significant consequences for some canopy-dwelling animal communities (Basham & Scheffers, 2020; Kuchenbecker et al., 2021). For instance, some insects show significant inter-seasonal variability, with greater species turnover observed in the forest canopy compared to the understory (Kuchenbecker et al., 2021). Similarly, canopy amphibian communities in the Panamanian rainforest are more vulnerable to changes in temperature and humidity than those on the forest floor, resulting in a migration to the ground to avoid desiccation during the dry season (Basham & Scheffers, 2020).

In conclusion, spatiotemporal changes in environmental conditions, together with several biotic factors, play a critical role in determining the distribution of species, their activity, and biotic interactions in the three-dimensional space of tropical rainforests. Thus, investigating the effect of these conditions is crucial for comprehending the distribution of biodiversity and ecological dynamics of these ecosystems. Papua New Guinea's pristine rainforests with high biodiversity make it an ideal location for this type of research.

1.2. Tropical ants and drivers of their distribution and activity

1.2.1. Ant diversity and function in tropical rainforests of Papua New Guinea

Ants (order Hymenoptera, family Formicidae) are an ecologically important and taxonomically diverse group of arthropods, inhabiting all strata of tropical rainforest (Basset et al., 1992; Lach et al., 2010). Papua New Guinea is a world-renowned centre of ant diversity, with over 900 species documented and probably many more waiting to be discovered (Fischer, 1960; Janda et al., 2016). The lowland forests of Papua New Guinea are particularly notable for their exceptional ant diversity, with over 120 species recorded in a single 0.04 ha plot, spanning multiple forest layers (Janda & Konečná, 2011).

In tropical lowland forests, ants contribute a significant proportion of animal biomass, accounting for up to 15% (Hammond, 1992). The dominance of ants is even more pronounced in the forest canopy, where they can constitute 20-70% of arthropod biomass (Tobin, 1995). Furthermore, ants perform a variety of functions, such as scavenging, predation, seed dispersal, decomposition, and herbivory (Basset et al., 1992; Lach et al., 2010; Wilkie et al., 2010; Del-Claro et al., 2018; Griffiths et al., 2018). Thus, given their exceptional biomass and involvement

in several biotic interactions, ants are often referred to as "ecosystem engineers" of tropical ecosystems (Lach et al., 2010).

1.2.2. Influence of environmental and biotic factors on species composition and foraging activity of ants in tropical rainforest

The species composition and foraging activity of ants are driven by the interplay between abiotic and biotic factors that exhibit considerable variability in space and time in tropical rainforests. Thus, these effects, in consequence, influence stratification and the ecological role of ants at spatiotemporal scales (Kaspari & Weiser, 2000; Hahn & Wheeler, 2002; Blüthgen & Stork, 2007; Houadria et al., 2014; Anjos et al., 2017; De Frenne et al., 2019).

As small ectotherms, ants are susceptible to variations in environmental conditions due to their small size and unfavourable surface-to-body volume ratio (Kaspari et al., 2015; Stark et al., 2017). As a result, ants can exhibit thermal overload and eventual dehydration (Bujan et al., 2016). Thus, changing environmental conditions, especially in temperature and humidity, over time and space influence ant activity and species composition at spatiotemporal scales (Cerdeira et al., 1998; Kaspari & Weiser, 2000; Hahn & Wheeler, 2002; Lasmar et al., 2021). Nevertheless, the effect of environmental conditions on different ant species may exhibit substantial intraspecific variability, given various morphological and physiological adaptations among ant communities (Kaspari et al., 2015; Bujan et al., 2016; Law et al., 2020). These traits, in conjunction with limiting conditions, determine the species' fundamental niche in the three-dimensional space of tropical rainforests (Kaspari & Weiser, 2000; Hahn & Wheeler, 2002; Kaspari et al., 2015; Leahy et al., 2020).

The realisation of this niche is further influenced by intraspecific/interspecific competition, and other biotic factors such as mutualistic interactions, and availability of resources (Philpott, 2010; Dáttilo et al., 2014; Falcão et al., 2014; Philpott, 2010; Anjos et al., 2017; Philpott et al., 2018). In tropical rainforests, direct and indirect competition for resources such as food and nesting sites seem to be a major factor contributing to the ant spatiotemporal distribution (Blüthgen et al., 2004; Blüthgen & Stork, 2007; Dáttilo et al., 2014; Philpott, 2010; Philpott et al., 2018). Nevertheless, the role of competition can vary a lot within different forest strata due to the uneven distribution of these resources across vertical space of tropical rainforest (Leston, 1973; Blüthgen & Stork, 2007; Dejean et al., 2007). As a result, canopy-dwelling ant communities are probably exposed to higher competition than ant communities

dwelling in lower strata, resulting in a more profound spatial distribution of ants in the forest canopy (Blüthgen & Stork, 2007; Wilkie et al., 2010).

In the tree canopies, ant communities, in contrast to lower strata, are predominantly organised by hierarchical dominance (Leston, 1970; Majer, 1972; Dejean et al., 2007). This dominance is established through competition, with individual ant species engaging in aggressive interactions (Majer, 1972). Thus, arboreal ants comprise a few dominant species exhibiting aggressive behaviour and the majority of ant biomass, alongside many subordinate species with low biomass and submissive behaviour (Majer, 1972; Leston, 1973; Dejean et al., 2007). As a result, dominant ant species often form exclusive territories through extensive competition for resources and limitation of the distribution of other dominant ants. This non-random arrangement of arboreal ant communities has been described as "ant mosaics" (Room, 1971; Majer, 1976). Furthermore, territorially dominant ants, nesting in various strata, regularly forage and interact with other ant species from distinct forest layers, modulating their foraging activity (Dejean et al., 2019; Tanaka et al., 2010). As a result, hierarchical dominance influences ant communities not just at spatial but also at temporal scales.

Additionally, fluctuations in resource availability also have a significant effect on ants (Blüthgen et al., 2003; Blüthgen & Stork, 2007; Dáttilo et al., 2014; Falcão et al., 2014). For instance, variations in the productivity of extrafloral nectaries and their spatial distribution are often associated with changes in ant competition, community structure, foraging activity, or even the formation of ant mosaics (alongside with hemipteran insects); (Blüthgen et al., 2000; Blüthgen & Stork, 2007; Falcão et al., 2014; Anjos et al., 2017; Del-Claro et al., 2018). In contrast, the influence of prey availability on tropical ants remains poorly understood. Nevertheless, it seems that temporal changes in the availability of prey may temporally shift ant foraging. Still, these fluctuations are probably highly intraspecific (Schöning et al., 2008; Molleman et al., 2016).

1.2.2.1. Vertical stratification and ecological differentiation of ants in the three-dimensional space of tropical rainforests

In tropical rainforests, ants exhibit a clear vertical stratification, leading to a partitioning of ant communities into three distinct forest strata: canopy, ground, and subterranean (Brühl et al., 1998; Wilkie et al., 2010). This vertical stratification is driven by varying environmental conditions and direct or indirect competition for limited resources, resulting in distinct ant communities with different ecology and physiological and morphological adaptations (Kaspari

& Weiser, 2000; Blüthgen et al., 2003; Wilkie et al., 2010; Kaspari et al., 2015; Bujan et al., 2016; Leahy et al., 2020).

Along the vertical space of tropical rainforests, ant communities exhibit distinct dietary ecology and nutrient limitations, given the availability of food resources (Davidson, 1997; Kaspari & Yanoviak, 2001, 2009). Canopy food webs are primarily plant-based, while food webs at lower layers, such as leaf litter, are detritus-based (Swift et al. 1979; Mattson, 1980; Pimm, 1982; Vitousek, 1982). Thus, despite most ant species being generalist omnivores, arboreal ant communities display a higher degree of specialization in plant-based resources with more substantial nitrogen limitations than terrestrial ant communities exploiting primarily animal-based resources with stronger carbohydrate restrictions (Blüthgen et al., 2003; Kaspari & Yanoviak, 2001). As a result, many arboreal ant species are assumed to be "cryptic herbivores", feeding as trophobionts or nectarivores on a carbohydrate-rich food. At the same time, ground-dwelling ant communities typically exhibit a more predatory diet (Blüthgen et al., 2003; Kaspari & Yanoviak, 2001, 2009). Nevertheless, Law et al. (2019) demonstrated using a cafeteria experiment that the dietary pattern of nitrogen limitation in the forest canopy may not be accurate for the entire ant community but rather for a numerical dominant species. The findings indicate that nutrient limitation in ants is highly intraspecific, even within ant communities in the same strata. However, competitive exclusion via dominant species, especially in the forest canopy, can have its role and cannot be disregarded.

Furthermore, caused by varying environmental conditions across the vertical forest strata, different ant communities exhibit distinct morphological and physiological adaptations (Kaspari et al., 2015; Bujan et al., 2016; Law et al., 2020). For instance, arboreal ants, are larger, darker and more heat/desiccation tolerant, enabling them to address challenging conditions of the forest canopies, including high levels of UV radiation, low humidity, and varying temperatures (Kaspari et al., 2015; Bujan et al., 2016; Law et al., 2020). In contrast, ants living in lower forest strata, where environmental conditions are relatively stable, are smaller with lighter cuticle, and lower heat/desiccation resistance (Kaspari et al., 2015; Law et al., 2020).

1.2.2.2. Diel foraging activity of ants in tropical rainforests

Ants, as small ectotherms, are subject to changes in environmental conditions influencing their foraging activity and species composition by altering their behaviour through overheating and desiccation (Cerda et al., 1998; Kaspari & Weiser, 2000; Hahn & Wheeler, 2002). Given their

physiological constraints, ants adapt their activity over time to suit favourable environmental conditions, resulting in spatiotemporal changes in their foraging activity (Cerda et al., 1998; Kaspari & Weiser, 2000; Hahn & Wheeler, 2002). For instance, in tropical rainforests, ant foraging is often associated with moisture gradients both at spatial and seasonal scales (Hahn & Wheeler, 2002; Kaspari & Weiser, 2000; Lasmar et al., 2021).

Nevertheless, that is probably not the case for the diel foraging activity as most of the ant communities across all forest strata of tropical rainforests possess higher foraging activity during the day with dryer and warmer conditions than at night (Anjos et al., 2017; Houadria et al., 2014; Seifert et al., 2016; Tanaka et al., 2010). This pattern is inconsistent with the vertical gradient of environmental conditions in the tropical rainforests and probably reflects distinct adaptations of vertically stratified ant communities and mild environmental conditions prevailing in the lower strata of tropical rainforests (Kaspari et al., 2015; Bujan et al., 2016; de Frenne et al., 2019; Law et al., 2020). Therefore, the diel foraging activity of ants in the tropical rainforests seems to be unaffected by diurnal variations of abiotic factors (Tanaka et al., 2010; Houadria et al., 2014; Seifert et al., 2016; Anjos et al., 2017).

Nonetheless, the diurnal prevailed foraging of ants may be explained by the physiological constraints associated with food availability and direct/indirect competition for such resources (Blüthgen et al., 2003; Baker-Méio & Marquis, 2012; Falcão et al., 2014; Houadria et al., 2014; Anjos et al., 2017). In tropical rainforests, most of the ant species are generalist omnivores, exhibiting various degree of specialization either towards plant-based or animal-based resources (Kaspari & Yanoviak, 2001; Blüthgen et al., 2003). Thus, diurnal fluctuations in quality and quantity of extrafloral nectar, abundance of trophobiotic insects, together with prey activity occurring in tropical ecosystems, which are often linked to diurnal variations of environmental conditions, could clarify the foraging patterns of ants in tropical rainforests (Basset et al., 2001; Baker-Méio & Marquis, 2012; Anjos et al., 2017). In addition, competition for valuable food resources could be also significant (Blüthgen et al., 2004; Blüthgen & Stork, 2007; Anjos et al., 2017). For instance, Anjos et al. (2017) demonstrated that in Brazilian Cerrado, intraspecific aggressiveness of ants was influenced by the quality of extrafloral nectar produced during the day, resulting in ant species turnover between day/night and prevailing diurnal ant foraging with lower species richness during the day. Therefore, the effect of biotic factors presumably has a crucial role in diurnal ant foraging and stratification of ant species in tropical ecosystems.

However, the effects of environmental factors still cannot be disregarded as all previous studies addressing the diel foraging activity of ants have been conducted just in primary forests, not secondary forests. Secondary forests, due to their lower canopy height and complexity, exhibit greater environmental extremes, especially in temperature and moisture which can potentially adjust ants foraging (Kaspari & Weiser, 2000; Tanaka et al., 2010; Ewers & Banks-Leite, 2013; Houadria et al., 2014; Seifert et al., 2016; Anjos et al., 2017; Sagar & Devy, 2022). Therefore, it is necessary to study the foraging activity of ants also in degraded habitats. Degraded habitats are increasingly prevalent and becoming an indispensable part of current tropical ecosystems due to extensive logging (Lewis et al., 2015). It is unknown, and remains to be investigated, whether the pattern of prevailed diel ant foraging, prevalent in tropical ecosystems, is a result of the activity of the entire ant community or primarily dictated by the activity of numerically dominant ant species, which can account for up to 90% of the total ant abundance (Tobin, 1997; Law & Parr, 2019).

2. Aims and scopes of the thesis

The aim of the thesis is to study the foraging activity of arboreal, semi-arboreal and terrestrial ant communities between day and night in primary and secondary tropical rainforests in Papua New Guinea and to investigate whether such foraging patterns are reflected by the activity of the entire ant community or dictated by numerically dominant ant species.

Specifically, we predicted:

- (i) Ant foraging activity would be generally higher during the day than at night.
- (ii) Ant foraging activity would show temporal differences between primary and secondary forests and their respective vertically stratified ant communities.
- (iii) Foraging activity of non-numerically dominant species would not reflect the foraging activity of numerically dominant species both across forest types and ant communities.
- (iv) Ant species would show distinct specialization towards diurnal or nocturnal foraging between the primary and the secondary forests.

3. Literature

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4. Manuscript

Diel Foraging Activity of Ants between Primary and Secondary Forests in Papua New Guinea

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4.1. Abstract

The three-dimensional structure of tropical rainforests, coupled with diel fluctuations in environmental conditions, generates environmental gradients affecting species composition and activity across spatiotemporal scales. Despite being small ectotherms, ants display consistent diurnal foraging across all forest strata, indicating their independence from diel environmental fluctuations. Nevertheless, whether this pattern persists in the harsher conditions of secondary forests remains unknown. Here we study the variations in diel ant foraging of vertically stratified ant communities between primary and secondary forests in Papua New Guinea. Using tuna baits, we sampled ant communities of disturbed and pristine forests during day and night. We found that the diel foraging activity of ants, although predominantly diurnal both in primary and secondary forests, exhibits considerable variation within and among ant communities. Specifically, in contrast to ant communities dwelling in lower forest strata, arboreal dwelling ants showed significantly higher foraging activity during the day than at night in primary but not secondary forests. In addition, the overall foraging patterns within ant communities were dictated by, predominantly diurnal, numerically dominant ant species. In contrast, non-numerically dominant ants exhibited predominantly cathemeral foraging behaviour both in primary and secondary forests. Nonetheless, whether such variations in diel foraging within ant communities were induced by interspecific physiological constraints or competition is unknown and remains to be investigated. Overall,

our study contributes to a better understanding of the ecological mechanisms underlying ant foraging patterns in tropical rainforests, which may have broader implications for the functioning of these complex ecosystems.

4.2. Introduction

Tropical rainforests form a complex, three-dimensional structure with a steep vertical gradient of varying resources and environmental conditions (Ozanne et al., 2003; De Frenne et al., 2019). As an environmental modulator, dense canopy vegetation protects the lower strata of the forest from solar radiation, creating a more stable, cooler, and humid climate in contrast to the upper layers (De Frenne et al., 2019). This results in environmental gradients that can be many orders of magnitude higher than those driven by latitude or altitude (Scheffers et al., 2013, 2014). As a result, the tropical rainforest's three-dimensional structure, with its environmental conditions, contributes to niche diversification and creates a microgeographical pattern of species distribution, known as vertical stratification (Brühl et al., 1998; Wilkie et al., 2010; Oliveira & Scheffers, 2019).

Additionally, tropical rainforest climatic conditions exhibit diurnal and seasonal fluctuations, marked by shifts in precipitation, temperature, and humidity over diurnal and seasonal scales (Park, 2003). These shifts in environmental conditions create an additional environmental gradient that, through physiological constraints, results in the partitioning of species not just in space but also in time (Hahn & Wheeler, 2002; Lee et al., 2014; Basham & Scheffers, 2020; Kuchenbecker et al., 2021). Given the large variability of environmental conditions, the temporal fluctuations have a greater impact on the tree canopy, in contrast to the understory of tropical rainforests, which is more stable and protected (Lee et al., 2014; Basham & Scheffers, 2020; Kuchenbecker et al., 2021).

In many tropical ecosystems, ants are the most common and dominant arthropods, living in all forest strata and fulfilling a range of ecological roles that classify them as ecosystem engineers (Basset et al., 1992; Wilkie et al., 2010; Del-Claro et al., 2018; Griffiths et al., 2018). As small ectotherms, ants are susceptible to variations in environmental conditions due to their small size and unfavourable surface-to-body volume ratio (Kaspari et al., 2015b; Stark et al., 2017). As a result, ants can exhibit thermal overload and eventual dehydration (Bujan et al., 2016). Thus, changing environmental conditions, especially in temperature and humidity, over time and space influence ant activity and species composition

at spatiotemporal scales (Cerda et al., 1998; Kaspari & Weiser, 2000; Hahn & Wheeler, 2002; Lasmar et al., 2021).

Given their physiological constraints, ants adapt their activity over time to suit favourable environmental conditions, resulting in spatiotemporal changes in their foraging (Cerda et al., 1998; Kaspari & Weiser, 2000; Hahn & Wheeler, 2002). For instance, in tropical rainforests, ant foraging activity is often associated with moisture gradients both at spatial and seasonal scales (Hahn & Wheeler, 2002; Kaspari & Weiser, 2000; Lasmar et al., 2021). Nevertheless, that is probably not the case for diurnal ant foraging as most of the ant communities across all forest strata of tropical rainforests exhibit higher foraging activity during the day than during night (Tanaka et al., 2010; Houadria et al., 2014; Seifert et al., 2016; Anjos et al., 2017). This pattern is inconsistent with the vertical gradient of environmental conditions in the tropical rainforests and probably reflects distinct adaptations of vertically stratified ant communities (Kaspari et al., 2015; Bujan et al., 2016; De Frenne et al., 2019; Law et al., 2020). For instance, arboreal ants are larger, darker, and more heat/desiccation tolerant, enabling them to address challenging conditions of the forest canopies (Kaspari et al., 2015; Bujan et al., 2016; Law et al., 2020). In contrast, ants living in lower forest strata, where environmental conditions are relatively stable, are smaller with lighter cuticle, and lower heat/desiccation resistance (Kaspari et al., 2015b; Law et al., 2020). Therefore, the diel foraging activity of ants in the tropical rainforests appears to be unaffected by diurnal variations of environmental conditions, as a result of well adapted ant species living in the forest canopy and mild environmental conditions prevailing in the lower strata of tropical rainforests (Kaspari et al., 2015; Bujan et al., 2016; De Frenne et al., 2019; Law et al., 2020). Further, the diurnal prevailed activity observed in ant communities within tropical ecosystems across all forest strata is likely to be more connected to biotic factors such as diel fluctuations in food availability, as well as the competition among ants for these resources (Blüthgen et al., 2003; Baker-Méio & Marquis, 2012; Falcão et al., 2014; Houadria et al., 2014; Anjos et al., 2017).

Nevertheless, the effects of environmental factors still cannot be disregarded as all previous studies addressing the diel foraging activity of ants have been conducted just in primary forests, not secondary forests. Secondary forests, due to their lower canopy height and complexity, exhibit greater environmental extremes, especially in temperature and humidity which can potentially adjust ants foraging (Kaspari & Weiser, 2000; Tanaka et al., 2010; Ewers & Banks-Leite, 2013; Houadria et al., 2014; Seifert et al., 2016; Anjos et al., 2017;

Sagar & Devy, 2022). Therefore, it is necessary to study the foraging activity of ants also in by logging degraded habitats, which are increasingly prevalent and are an indispensable part of current tropical ecosystems (Lewis et al., 2015). Additionally, whether the pattern of prevailed diel ant foraging, prevalent in tropical ecosystems, is a result of the activity of the entire ant community or primarily dictated by the activity of numerically dominant ant species, which can account for up to 90% of the total ant abundance, is unknown and remains to be investigated (Tobin, 1997; Law & Parr, 2019).

Here, we studied the foraging activity of arboreal, semi-arboreal and terrestrial ant communities between day and night in primary and secondary tropical rainforests in Papua New Guinea. In addition, we investigated whether such foraging patterns are reflected by the activity of the entire ant community or dictated by numerically dominant ant species.

Specifically, we predicted:

- (i) Ant foraging activity would be generally higher during the day than at night.
- (ii) Ant foraging activity would show temporal differences between the primary and the secondary forests and their respective vertically stratified ant communities.
- (iii) Ant species would show distinct specialization towards diurnal or nocturnal foraging between the primary and the secondary forests.
- (iv) Foraging activity of non-numerically dominant species would not reflect the foraging activity of numerically dominant species both across forest types and vertically stratified ant communities.

4.3. Materials and Methods

4.3.1. Study sites

The fieldwork was conducted at two sites in a lowland evergreen rainforest in Madang Province, Papua New Guinea. The experimental sites were located in two isolated forest fragments of primary forest near the villages of Baiteta and Baitabag (5°01.73'S, 145°46.01'E, 40 - 80 m. a.s.l, 1200 ha; 5°07.99'S, 145°45.47'E, 40-80 m. a.s.l, 600 ha respectively; Figure S1), and their respective secondary forests. The fragments are surrounded by secondary forests which were clear-cut in 1970's, and by a relatively densely populated, agriculturally exploited landscape, including abandoned gardens, rural settlements, and plantations. The climate is humid, with an annual rainfall average of 3600 mm, an average air temperature of 26.5 °C, and a moderate dry season from June to September (McAlpine et al., 1983).

4.3.2. Sampling design and ant collection

Towards the end of the dry season in September and early October 2021, we randomly selected 16 transects within each experimental site, eight in the primary and eight in the secondary forest (i.e., 32 transects in total in the two experimental sites). Along each of these transects, we selected five individuals of different tree species with an approximate DBH of 20 cm. Individual trees were roughly 50 m from each other, while individual transects were at least 200 m apart (Figure S2, A,B). All transects were located at least 50 m from the forest edge.

To determine any differences in foraging activity and species composition of ants from different forest strata during the day and night, we used baits made from commercially canned tuna in sunflower oil. Crushed tuna meat was baited under a strip of square pieces of gauze (10 x 10 cm). At each of the five focal trees of each transect, we attached one bait to the bark of the tree trunk at breast height and placed another one on the forest floor 2 m from the focal tree (i.e., a total of 10 baits per transect and 640 baits across two experimental sites and day/night; Figure S2, B,C). Trunk baits were secured with pins, and ground baits were set, so the gauze corners were weighted down to allow ants to easily run over the bait's edges. We exposed baits always at either 9 AM or 9 PM and checked them after 1 h (i.e., at 10 AM or 10 PM) to survey the day-time and night-time species specialization and activity of ants respectively. We maintained a 24-h interval between day and night collection on a given transect to avoid potential disturbance from previous bait placement. Therefore, four transects were set and collected each morning, another four transects were set and collected at night of the same day. Sampling was carried out only in sunny or favourable weather conditions.

During the checks, we counted (>50 individuals) or estimated the number of workers of each morphospecies observed at each of the baits. We collected at least five individuals into a vial filled with 95% ethanol for future identification and ecological niche assignment. Ants were always counted/estimated and collected only from the top side of the 10 × 10 cm gauze square without disturbing the remaining ants.

4.3.3. Species and niche identification

We assigned all ants to genus according to a published taxonomic key (Bolton, 1994) then identified all individuals to morphospecies or species using online image databases (www.antweb.org; www.newguineants.org) and the reference collection of the Biological

Centre of the Czech Academy of Sciences (BC CAS). All voucher specimens were deposited at the Institute of Entomology, BC CAS, in the Czech Republic.

Afterwards, we classified each ant morphospecies or species into its "vertical foraging niche" based on its nesting preference and foraging activity within the vertical space of the tropical rainforest. The guild included three categories: arboreal, semiarboreal, and terrestrial. The assignment of ecological niches was based on the literature and other ecological surveys of ants. Particularly, we used data from felling projects conducted in Papua New Guinea in the past (Klimes et al., 2012; AntWiki, 2023; Klimes unpublished data).

4.3.4. Statistical analyses

The effectiveness of our sampling was assessed by species accumulation curves and Chao 2 estimator in EstimateS 9.1.0. (Colwell & Elsensohn, 2014). Specifically, we constructed the sample-based species accumulation curves based on the recorded/estimated ant morphospecies abundance on each bait designed separately for day and night sampling both in the primary and the secondary forests. Then, we compared the observed number of ant species occurring in each combination of sampling units with non-parametric estimator Chao 2 (Chao et al., 2005; Colwell & Elsensohn, 2014).

To test the level of specialization for diurnal/nocturnal foraging of ants between the primary and the secondary forests, we used bipartite ecological interaction networks (Blüthgen et al., 2006; Dormann et al., 2008; Dormann, 2011). First, we created a contingency matrix summarizing the number of cases of each ant species occurring on baits either during the day or night ($N = 150$). Then, we calculated the two-dimensional Shannon entropy (H_2), a network specialization index ranging from 0 (indicating low interaction specificity) to 1 (indicating high interaction specificity), to assess the degree of specialization in the overall network separately for the primary and the secondary forests (Blüthgen et al., 2006). Consequently, we tested the Shannon entropy (H_2) of each forest type against a null model to investigate the significance of network-level specialization. The null models were constructed using the Patefield algorithm resulting in null models based on 1000 randomized networks exhibiting the same number of interactions and the same marginal totals as the original network (Patefield, 1981; Blüthgen et al., 2006; Wehner et al., 2018). All interaction network analyses were obtained using a *bipartite* package in R 4.1.3. (Dormann et al., 2008; Dormann, 2011; R Core Team., 2023).

The generalized mixed-effects models (GLMM) with an assumed Poisson distribution and a logit link function were applied to analyse variations in ant diurnal foraging among numerically and non-numerically dominant ant communities from all forest strata and different forest types. Specifically, we constructed two distinct models, including records of either the non-numerically dominant ant morphospecies or all ant morphospecies pooled. Numerically dominant ant morphospecies were defined as those accounting for 90% of the total ant abundance, while non-numerically dominant ants were defined as those accounting for the remaining 10% (Law & Parr, 2019). As a response variable, we used estimated/recorded ant abundance, assigned as a proxy of ant foraging, per guild occurring on baits (N = 806, all morphospecies pooled; N = 359, non-numerically dominant morphospecies), while as explanatory variables (fixed effects), we used the factor of time (day, night), forest type (primary forest, secondary forest), and guild (arboreal, semiarboreal, terrestrial), and their respective interactions. To account for potential temporal and spatial autocorrelation within tree individuals and localities, we assigned tree and site identities as random effects. Additionally, in the case of a model suffering from overdispersion, we included a random effect capturing variability at the level of individual observations. To evaluate the performance of models and to test the effect of individual predictors, we used the likelihood ratio tests (LRT). Specifically, we compared the null models with a series of more complex models including random effects, fixed effects, and their interactions. Afterwards, we applied the non-parametric post hoc Tukey HSD tests to test differences within individual interactions. All models and analyses were created and performed in R 4.1.3 using *lme4* and *multcomp* package (Hothorn et al., 2008; Bates et al., 2015; R Core Team., 2023).

4.4. Results

We recorded/estimated 212,310 ant individuals belonging to 75 distinct morphospecies, 30 genera, and six subfamilies (see Table S1). Out of the total of 640 exposed baits, 552 were occupied by ants. Eight morphospecies belonging to eight genera (*Wasmania*, *Carebera*, *Crematogaster*, *Technomyrmex*, *Philidris*, *Pseudolasius*, *Oecophylla*, and *Papyrius*) accounted for 90% of the total ant abundance, while 67 morphospecies, belonging to 23 genera, accounted for the remaining 10% of the recorded ant individuals (Figure S3). In primary forests, based on species accumulation curves, the estimated number of observed species was higher during the day (mean = 47, 95% CI [37.8, 56.2]) than at night (37, 95% [31.65, 42.35]). Nevertheless, according to Chao2 estimates, the total number of species

occurring in primary forests was much higher than the number of species estimated in our samples, especially during the day (81.28, 95% [59.34, 142.28]), to a lesser extent at night (44.75, 95% [39.11, 65.45]; Figure 1A, C). In contrast to primary forests, the estimated number of species observed in secondary forests was higher at night (32, 95% [25.57, 38.43]) than during the day (25, 95% [19.75, 30.25]). Chao2 estimates for the total number of species occurring in secondary forests was relatively low, with estimates of 44.92 species 95% [35.68, 77.37] at night and 32.16 species 95% [26.59, 57.19] during the day (Figure 1B, D).

In primary forests, ants exhibited a high degree of specialisation either towards diurnal or nocturnal foraging ($H2' = 0.27$). In addition, network-level interaction specificity of ants between day and night in the primary forests differed significantly from the random network models, illustrating a substantial specialization of ant foraging activity between the two time periods ($p < 0.001$; Figure 2). We detected a strict preference for diurnal foraging for 13 morphospecies from six genera (*Pachycondyla*, *Pheidole*, *Polyrhachis*, *Rhytidoponera*, *Solenopsis*, and *Vollenhovia*), and we observed 11 ant morphospecies belonging to eight genera (*Camponotus*, *Crematogaster*, *Odontomachus*, *Pheidole*, *Podomyrma*, *Strumigenys*, *Technomyrmex*, *Tetramorium*) to be active only at night (Figure 2). In contrast, in the secondary forests, the degree of diurnal/nocturnal foraging specialization was low ($H2' = 0.06$), and the network-level interaction specificity of ants between day and night was not significantly different from the random networks, indicating no significant differentiation in diurnal/nocturnal ant foraging ($p = 0.2$; Figure 3). Conversely to the primary forests, we observed a decrease in the number of strictly diurnal active morphospecies, with only six morphospecies from five genera (*Camponotus*, *Paratrachina*, *Pheidole*, *Polyrhachis*, *Tetramorium*) being active during the day. Nevertheless, during the night, the number of strictly nocturnal active morphospecies slightly increased from 11 to 13 morphospecies belonging to eight genera (*Camponotus*, *Carebara*, *Crematogaster*, *Pheidole*, *Polyrhachis*, *Solenopsis*, *Tetramorium*, *Anochetus*; see Figure 3). In addition, some ant morphospecies found in both forest types showed changes in their foraging from diurnal specialists in primary forests to cathemeral foragers (with no distinct diurnal or nocturnal activity pattern) in secondary forests (Phei 010, Oeco 001; Figure 2, 3).

When examining the variation in diurnal foraging activity of ants within the whole ant community (including all numerically and non-numerically dominant ant morphospecies), we found that ant foraging activity was significantly higher during the day than at night ($\beta = 0.523$, $X^2 = 10.305$, $P = 0.001$; Figure 4A). However, this foraging pattern was led by eight

numerically dominant ant morphospecies, representing 90% of the ant abundance recorded on baits, as non-numerically dominant ants, representing the majority of ant diversity (i.e., 67 out of 75 ant morphospecies), did not significantly differ in their diurnal foraging ($X^2 = 2.365$, $P = 0.124$; Figure 4B). Similar variations in the foraging activity within ant communities were also observed between different forest types. We found significantly higher overall ant foraging activity in the secondary forests compared to the primary forests for the entire ant community ($\beta = 0.111$, $X^2 = 5.265$, $P = 0.022$). Nevertheless, this difference was not observed in the foraging activity of ant communities that were not numerically dominant ($X^2 = 0.601$, $P = 0.439$). In addition, we found a significant difference in ant abundance within ant guilds for both numerically and non-numerically dominant ant morphospecies ($X^2 = 50.335$, $P < 0.001$; $X^2 = 152.901$, $P < 0.001$). Specifically, semiarboreal ants were the most abundant compared to other guilds in the case of whole ant community, while terrestrial ants were the most abundant in the case of non-numerically dominant ant morphospecies.

Interestingly, we did not find a significant difference in daily ant foraging between individual forest types and nesting guilds both for numerically ($X^2 = 4.462$, $P = 0.107$) and non-numerically dominant ant communities ($X^2 = 2.241$, $P = 0.524$; Table 1). Nonetheless, after further examination of the interactions using the non-parametric post hoc Tukey HSD tests, we did find a significant difference in the diurnal ant foraging, but just in the case of arboreal ants, exhibiting higher foraging activity during the day than at night ($\beta = 1.433$, $Z = -3.893$, $P = 0.001$; Figure 5; Table S2). In contrast, the arboreal ant communities that were not numerically dominant did not display significant distinction in their foraging activity ($Z = -0.960$, $P = 0.904$; Figure 6; Table S2). Not significant effects were also observed in the case of other guilds (semiarboreal and terrestrial ants) and two different forest types (primary and secondary forest) both for the non-numerically dominant ant morphospecies and all morphospecies pooled (Figure 5, 7; Table S2). Furthermore, we found a significant interaction between time, vertical foraging guild and forest type both for numerically and non-numerically dominant ant communities ($X^2 = 19.264$, $P = 0.007$; $X^2 = 223.971$, $P < 0.001$). Specifically, at the level of the whole community, we observed a distinctive change in ant foraging between the primary and the secondary forests only in arboreal dwelling communities, which exhibited significantly higher ant foraging during the day than at night in the primary forests but not in the secondary forests ($\beta = 1.641$, $Z = -3.433$, $P = 0.028$; $Z = 0.675$, $P = 0.999$, Figure 7). In contrast, in the case of non-numerically dominant ants, arboreal ant communities did not show a significant difference in their foraging activity between different forest types ($Z = 0.010$, P

= 1.000; $Z = -1.351$, $P = 0.943$, Figure 8). Similar patterns were also noted in terrestrial ant communities ($Z = -1.237$, $P = 0.969$; $Z = -0.656$, $P = 0.999$, Figure 8), but not in the case of semiarbooreal ants exhibiting significantly higher foraging activity during the day in the primary forests ($\beta = 0.901$, $Z = -3.382$, $P = 0.019$; Figure 8), but not in the secondary forests ($Z = 2.616$, $P = 0.177$; Figure 8)

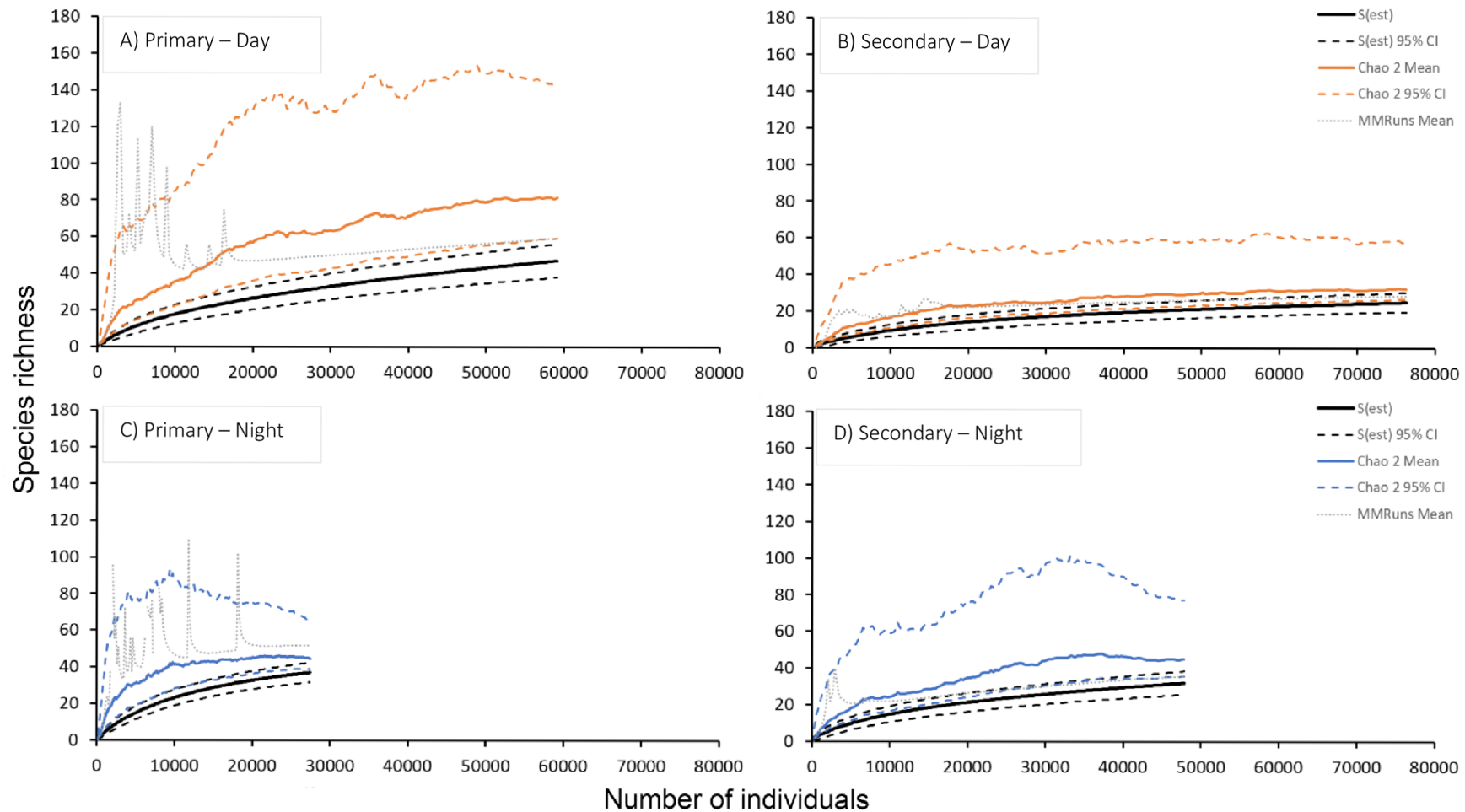


Figure 1: Species accumulation curves (estimated) with 95% confidence intervals (CI) and with Chao2 estimator with 95% confidence intervals (CI); A = Primary forests, Day; B = Secondary forests, Day; C = Primary forests, Night; D = Secondary forests, Night; S(est) = estimated number of species; Chao2 mean = average estimate of the total number of species; MMRuns Mean = the mean value of the number of species accumulated across multiple Monte Carlo simulations.

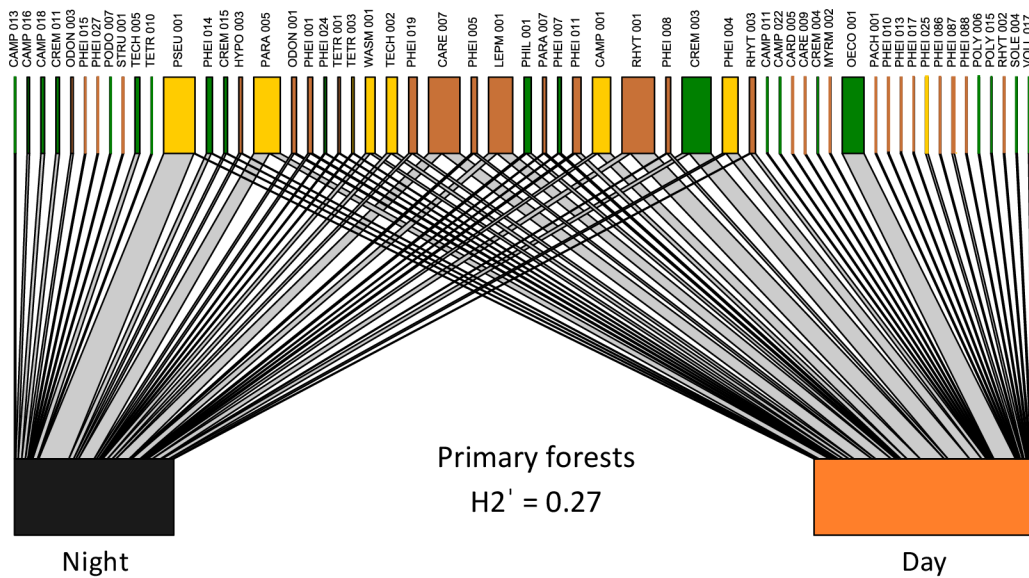


Figure 2: The bipartite network graph representing a degree of specialization for diurnal or nocturnal foraging of 58 ant morphospecies recorded in the primary forests of Papua New Guinea. The morphospecies are depicted by the upper blocks that exhibit three colors signifying three stratified guilds (green = arboreal, yellow = semiarboreal, brown = terrestrial). The lower blocks exhibit two colors representing the time when the morphospecies occurred (black = night, orange = day). The width of links and upper blocks indicate the number of occurrences of the morphospecies detected in total and between day/night, while the lower box widths show overall occurrence during day/night. For more information about individual morphospecies (species, subfamily) see TableS1.

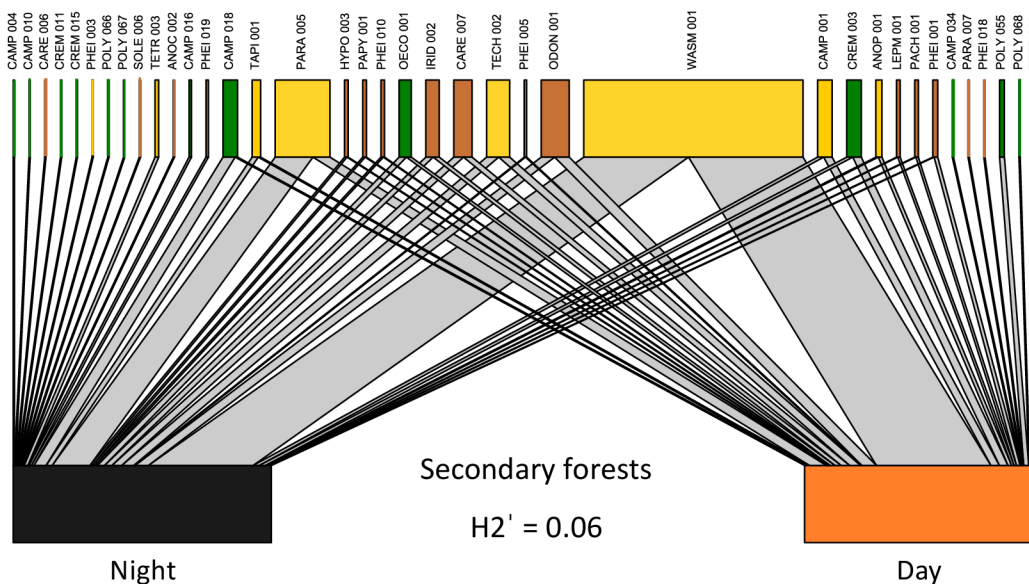


Figure 3: The bipartite network graph representing a degree of specialization for diurnal or nocturnal foraging of 38 ant morphospecies recorded in the secondary forests of Papua New Guinea. The morphospecies are depicted by the upper blocks that exhibit three colors signifying three stratified guilds (green = arboreal, yellow = semiarboreal, brown = terrestrial). The lower blocks exhibit two colors representing the time when the morphospecies occurred (black = night, orange = day). The width of the links and blocks indicate the number of occurrences of the morphospecies detected in total and between day/night, while the lower box widths show their overall occurrence during day/night. For more information about individual morphospecies (species, subfamily) see TableS1.

Table 1: Likelihood-ratio tests of the three focal predictors and their interactions on the foraging activity (abundance) of the whole ant community (A) and the non-numerically dominant ant community (B) recorded on baits in the tropical rainforests of Papua New Guinea.

A.	Predictors	X^2 statistic	Df	P value
	Time	10.305	1	<u>0.001</u>
	Forest Type	5.265	1	<u>0.022</u>
	Nesting Guild	50.355	2	<u>< 0.001</u>
	Time: Forest Type*	4.462	2	0.107
	Time: Nesting Guild*	7.556	2	0.229
	Time: Nesting Guild: Forest Type*	19.264	7	<u>0.007</u>
B.				
	Time	2.365	1	0.124
	Forest Type	0.601	1	0.439
	Nesting Guild	152.901	2	<u>< 0.001</u>
	Time: Forest Type*	2.241	3	0.524
	Time: Nesting Guild*	7.483	3	0.058
	Time: Nesting Guild: Forest Type*	223.971	6	<u>< 0.001</u>

Notes: Df represents degrees of freedom; P is the type I error probability estimate; * see Table S2, S3, S4. for the results of the mean differences between the levels within variables contributing to interactions.

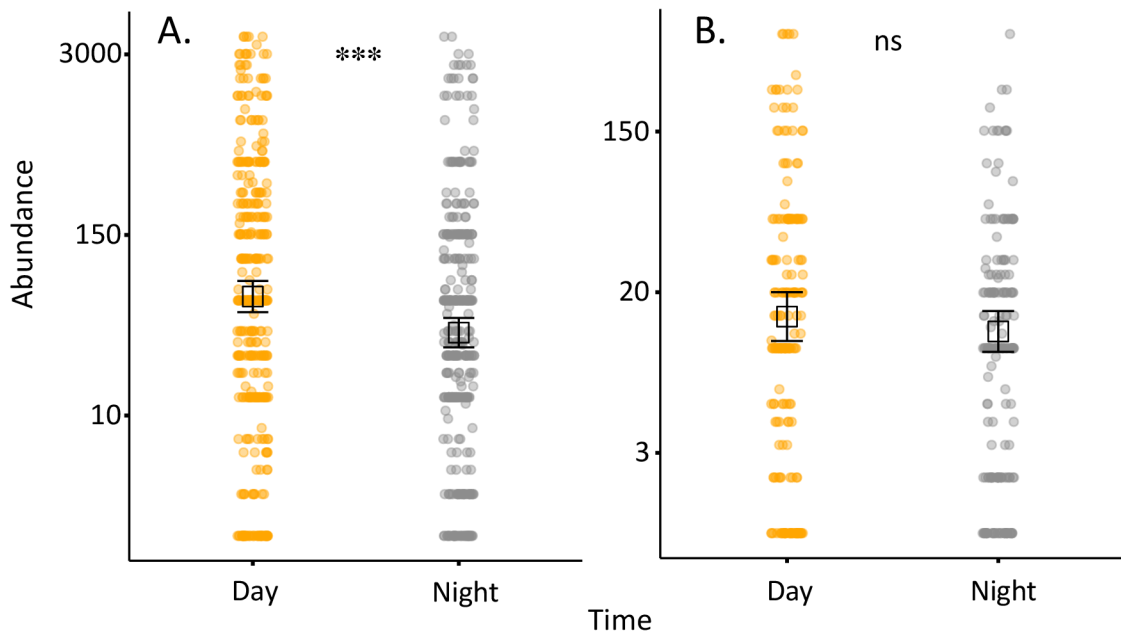


Figure 4: The effect of time (day, night) on the foraging activity (abundance) of the whole ant community (A) and the non-numerically dominant ant community (B) recorded on baits. Small dots represent raw values of individual abundance estimates; the whiskers show the predicted means with 95 % confidence intervals implied by the fitted GLMM model. The y-axes are plotted with raw values on a natural logarithmic scale; The significant and nonsignificant results are indicated by *** (≤ 0.001); ns (≥ 0.05).

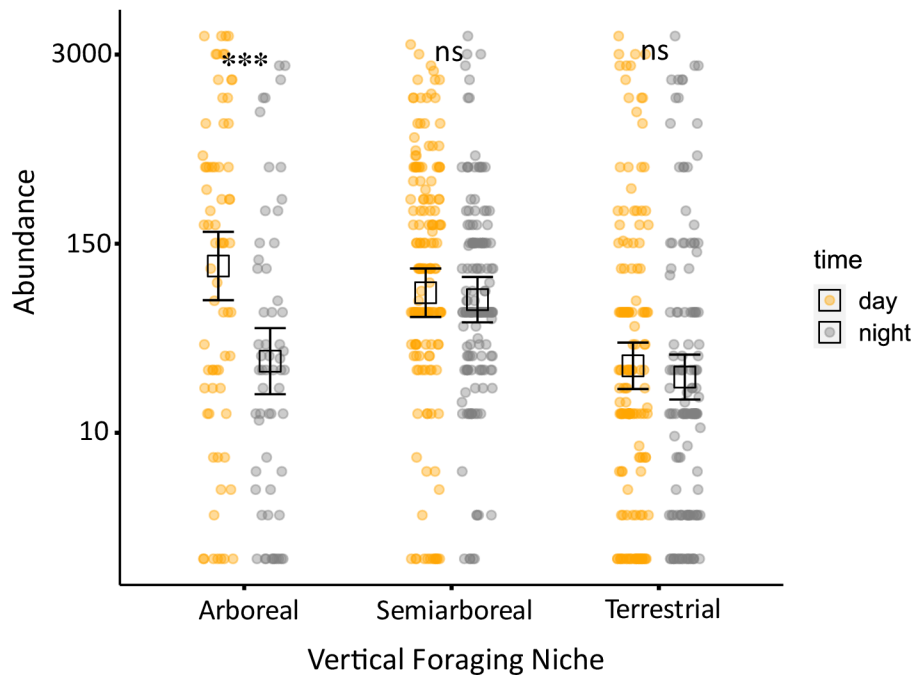


Figure 5: The effect of the vertical foraging niche (arboreal, semiarboreal, terrestrial) on the foraging activity (abundance) of the whole ant community recorded on baits. Small dots represent raw values of individual abundance estimates; the whiskers show the predicted means with 95 % confidence intervals implied by the fitted GLMM model. The y-axis is plotted with raw values on a natural logarithmic scale; The significant and nonsignificant results are indicated by *** (≤ 0.001); ns (≥ 0.05).

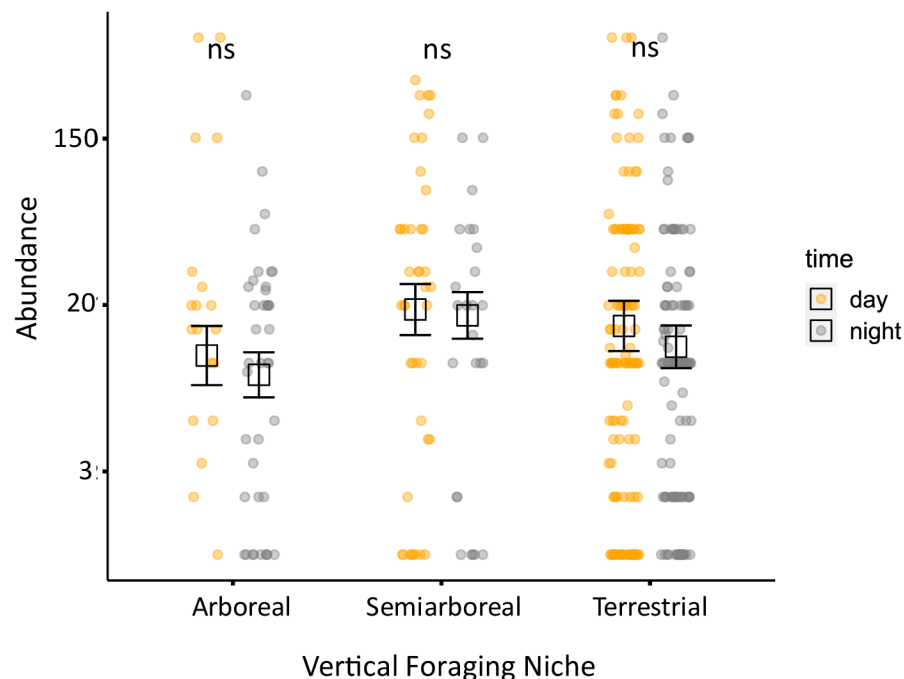


Figure 6: The effect of the vertical foraging niche (arboreal, semiarboreal, terrestrial) on the foraging activity (abundance) of the non-numerically dominant ant community recorded on baits. Small dots represent raw values of individual abundance estimates; the whiskers show the predicted means with 95 % confidence intervals implied by the fitted GLMM model. The y-axis is plotted with raw values on a natural logarithmic scale; The nonsignificant results are indicated by ns (≥ 0.05).

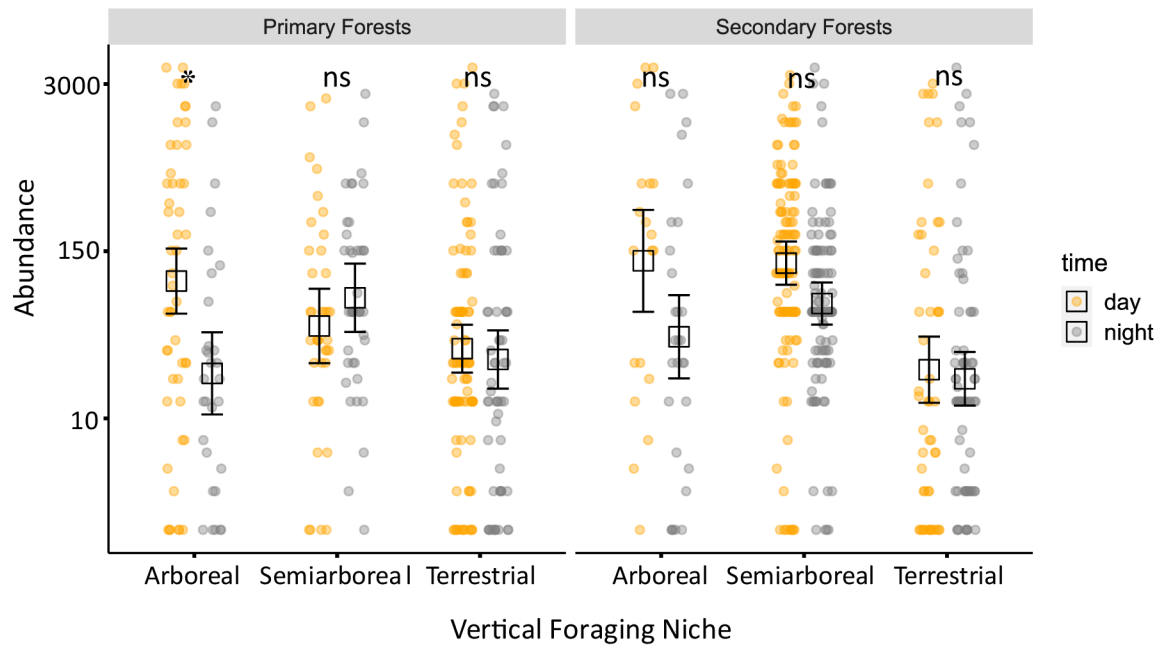


Figure 7: The effect of the vertical foraging niche (arboreal, semiarboreal, terrestrial) on the foraging activity (abundance) of the whole ant community recorded on baits between the primary and the secondary forests. Small dots represent raw values of individual abundance estimates; the whiskers show the predicted means with 95 % confidence intervals implied by the fitted GLMM model. The y-axis is plotted with raw values on a natural logarithmic scale; The significant and nonsignificant results are indicated by * (≤ 0.05); ns (≥ 0.05).

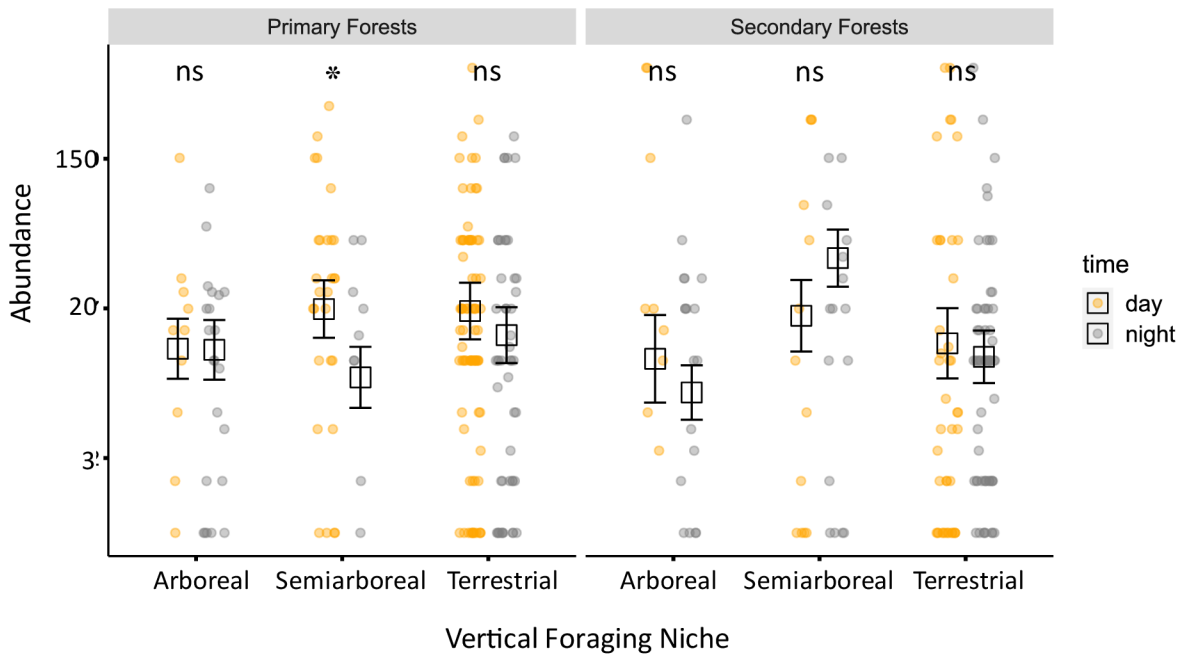


Figure 8: The effect of the vertical foraging niche (arboreal, semiarboreal, terrestrial) on the foraging activity (abundance) of the non-numerically dominant ant community recorded on baits between the primary and the secondary forests. Small dots represent raw values of individual abundance estimates; the whiskers show the predicted means with 95 % confidence intervals implied by the fitted GLMM model. The y-axis is plotted with raw values on a natural logarithmic scale; The significant and nonsignificant results are indicated by * (≤ 0.05); ns (≥ 0.05).

4.5. Discussion

The diel foraging patterns of ants between primary and secondary tropical forests with different environmental conditions have not been previously investigated. In this study, we therefore examined the variations in diurnal ant foraging within and among vertically stratified ant communities living in two distinct forest types. We found that the foraging activity at the level of the whole ant community was significantly higher during the day than at night. This prevailed diurnal foraging of ants found in our study is consistent with the results documented by Houadria et al. (2014) and Seifert et al. (2016). Collectively, our findings indicate that the diel foraging activity of ants in tropical rainforests is not significantly influenced by diel variations in environmental conditions. This conclusion is further supported by observed foraging patterns of vertically stratified ant communities. Similar to Tanaka et al. (2010), we observed that arboreal dwelling ant communities, as the only guild, showed significantly higher foraging activity during the day than at night. Such foraging patterns are in contrast to the vertical gradient of environmental conditions, as forest canopies in tropical rainforests exhibit extreme conditions both in temperature and humidity in contrast to the lower forest strata (De Frenne et al., 2019; Basham & Scheffers, 2020). Nonetheless, as was demonstrated in other studies, vertically stratified ant communities show distinct adaptations, which probably enable them to address such challenging conditions. For instance, arboreal dwelling ants are more resilient to environmental extremes occurring in the forest canopy than ants living in the relatively stable lower forest layers of tropical rainforests (Kaspari et al., 2015; Bujan et al., 2016; De Frenne et al., 2019; Basham & Scheffers, 2020; Law et al., 2020). Therefore, observed prevailing diurnal ant foraging is probably a result of well adapted ant species living in the forest canopy and mild environmental conditions occurring in the lower strata of tropical rainforests (Kaspari et al., 2015; Bujan et al., 2016; De Frenne et al., 2019; Law et al., 2020).

In addition, similar foraging patterns were also noted in disturbed habitats susceptible to environmental extremes. Specifically, we found no significant change in ant foraging behaviour at the level of the whole ant community between day and night in secondary forests compared to pristine primary forests (Table S2). This result contradicts our hypothesis that ant foraging activity would show temporal differences between primary and secondary forests and indicates a strong resilience of secondary forest ant communities to harsh environmental conditions. Indeed, Leong et al. (2022) showed that ground dwelling ant communities living in rubber plantations in Thailand exhibited greater heat tolerance than ant communities found in less disturbed habitats, where the conditions are more stable than in rubber plantations. If

this is also the case for the secondary forest ant communities, their potentially greater resilience to extreme environmental conditions may contribute, and partly explain, the prevailing diurnal foraging patterns of ants observed in our study. However, this may not be the case for the entire ant community, as diel foraging activity of arboreal ant communities varied (Table S3). In particular, arboreal dwelling ants showed significantly higher foraging activity during the day than at night in primary forests, but the strength of these foraging patterns was less pronounced in the secondary forests (Table S3). These findings imply that environmental conditions may still play a role in diel ant foraging, particularly in ant communities living in habitats with extreme environmental conditions such as the secondary forest canopies. Nonetheless, it is important to note that even though the difference in diel foraging activity of arboreal dwelling ant communities in the secondary forests was not significant, the ants were still predominantly diurnal (Table S3). Thus, a non-significant result in diel foraging of arboreal ants between primary and secondary forests can be just an artefact of the length of the sampling period in our study and momentary changes in biotic or abiotic factors at given sites. Therefore, based on our findings, we conclude that tropical rainforest ants at the community level, even though exhibiting some variations across vertically stratified ant communities, are predominantly diurnal both in primary and secondary forests regardless of distinct environmental conditions occurring between these two forest types.

The fact that ants in tropical rainforests foraged predominantly during the day may be attributed to diel fluctuations in food availability associated with physiological constraints caused by changes in environmental conditions (Basset, 2001; Falcão et al., 2014; Anjos et al., 2017). For instance, diel shifts in temperature and humidity can cause an alternation of plant phenology resulting in an increase of abundance and activity of herbivory insects, which subsequently affects predator-prey interactions (Schöning et al., 2008; Lee et al., 2014; Molleman et al., 2016; Anjos et al., 2017; Kuchenbecker et al., 2021). In tropical rainforests, most of the ant species are generalist omnivores, exhibiting various degree of specialization either towards plant-based or animal-based resources (Kaspari & Yanoviak, 2001; Blüthgen et al., 2003). For instance, arboreal ant communities display a higher degree of specialization in plant-based resources than terrestrial ant communities exhibiting primarily animal-based diet (Blüthgen et al., 2003; Kaspari & Yanoviak, 2001, 2009) Thus, diurnal variations in quality of extrafloral nectar, activity of trophobiotic insects, and prey availability, which is typically higher during the day than at night, could explain the predominantly diurnal foraging patterns of ants observed in our study (Basset, 2001; Baker-Méio & Marquis, 2012; Anjos et al., 2017).

Nevertheless, when examining diel foraging within ant communities, we found that observed ant foraging activity was strongly determined by the numerically dominant ant species. Specifically, at the level of the whole ant community, we found that the numerically dominant ant species, representing 90% of the recorded ant abundance, foraged significantly more during the day than at night, whereas the non-numerically dominant ant species, representing 10% of recorded ant abundance, did not significantly differ in their diel foraging. Similar foraging patterns were also observed in arboreal ant communities but not in semiarboreal and terrestrial dwelling ants, both for numerically and non-numerically dominant ant species, which exhibited more cathemeral behaviour. Such findings can be explained by two potential processes.

Firstly, the differences in ant foraging within the ant community may result from different physiological and morphological adaptations to environmental conditions among ant species. Specifically, tropical rainforest ants often show differences in their resilience to environmental conditions, even within ant communities from the same forest strata (Kaspari et al., 2015; Bujan et al., 2016). Thus, based on our results, we can hypothesise that a higher number of non-numerically dominant ant species were more physiologically constrained by high temperatures and low humidity levels during the day, leading to an increase in their nocturnal foraging and subsequently to the cathemeral foraging behaviour observed in our study.

Alternatively, different foraging patterns within ant communities can be a result of intense competition and subsequent niche differentiation (Stuble et al., 2013; Houadria et al., 2014; Grevé et al., 2019). In particular, niche differentiation among ants is often driven by competition for valuable food sources induced by behaviourally dominant ant species, which are also often the most abundant (Davidson, 1998; Morrison, 1996). Therefore, we hypothesise that the numerically dominant ant species may have excluded some non-numerically dominant ants during the peak period of resource availability (day), resulting in changes in their foraging behaviour towards the time with likely lower interspecific competition (night) and consequently to more prominent cathemeral foraging behaviour (Basset et al., 2001; Anjos et al., 2017).

In addition, these effects should be even stronger in the case of arboreal dwelling ant communities, as a result of extreme environmental conditions and the higher competition occurring in the forest canopies (Blüthgen & Stork, 2007; Wilkie et al., 2010; De Frenne et al., 2019; Basham & Scheffers, 2020). Indeed, we found that the shift in foraging activity among

numerically and non-numerically dominant ants was the most significant for arboreal ant communities but not for semiarboreal and terrestrial dwelling ants. Nevertheless, this was not the case for the foraging activity between primary and secondary forests, as we found strong shifts in ant foraging behaviour not just in arboreal ant communities but also in the case of semiarboreal ants, especially in primary forests. Specifically, non-numerically dominant, semiarboreal ant species showed opposite foraging activity to the numerically dominant, semiarboreal ants. Thus, as in arboreal dwelling ant communities, we assume that foraging patterns of non-numerically dominant, semiarboreal ants between primary and secondary forests were influenced by competition for food sources and physiological constraints induced by environmental conditions occurring between these two forest types.

Furthermore, we revealed that ant communities in primary forests displayed greater diurnal or nocturnal foraging specialization in contrast to ant communities in secondary forests (see Figure 2, 3). These foraging patterns are probably attributed to differences in structural complexity, stability and diversity between these two forest types (Corlett, 1995; Ewers & Banks-Leite, 2013; Sagar & Devy, 2022). Specifically, higher complexity, stability and diversity in pristine primary forests could potentially lead to greater and more persistent niche differentiation within ant communities, resulting in greater diurnal or nocturnal foraging specialisation in primary forests compared to less complex, diverse and stable secondary forests (Corlett, 1995; Sagar & Devy, 2022). In particular, we observed that secondary forests exhibit a lower number of diurnal foraging ant species, but a greater number of nocturnal foragers compared to primary forests. Additionally, we observed that some ant morphospecies found in both forest types showed changes in their foraging from diurnal specialists in the primary forests to cathemeral foragers in the secondary forests. These findings imply that environmental factors may favour the presence of specialised nocturnal species in more challenging conditions or induce behavioural thermoregulation, which is consistent with the observation of other studies (Andrew et al., 2013; Sunday et al., 2014). However, the impact of competition and other biotic factors contributing to such changes must be considered.

While our study provided a rare insights into the foraging activity of ant communities in primary and secondary forests, several caveats should be considered. First of all, the use of bait traps is inherently selective and do not represent the foraging patterns of entire ant community. Nonetheless, baiting is a recognised technique in the study of ant ecology and allowed us to efficiently map foraging activity of ants from different forest strata, a task that would be challenging using alternative methods (Blüthgen & Stork, 2007; Dejean et al., 2007).

Additionally, the lack of empirical data on environmental conditions such as temperature may have affected the accuracy of our conclusions. Nonetheless, measuring ambient temperature alone may not comprehensively assess the environmental conditions that affect ant communities in primary and secondary forests, as the heterogeneous nature of forest environments can impose various constraints on small ectotherms, such as ants, that are not fully captured by air temperature measurements (Kaspari et al., 2015; Scheffers et al., 2017; Stark et al., 2017). Therefore, additional factors such as microclimatic variability and habitat structure should be considered to fully understand the complex environmental factors shaping ant foraging in different forest types. However, logistical constraints prevented us from incorporating such factors in our study. Thus, future investigations that account for these factors are needed to advance our understanding of diel foraging ant activity in forest ecosystems.

4.6. Conclusion

Our study provides novel insights into the diel foraging patterns of ants in tropical rainforests, revealing variations across vertically stratified ant communities in primary and secondary forests with different environmental conditions. Specifically, we found that at the community level the foraging activity of ants in tropical rainforests was predominantly diurnal. This foraging behaviour was consistent with minor changes across all vertically stratified ant communities and between primary and secondary forests, indicating the strong resilience of tropical ants to environmental conditions. Nevertheless, these foraging patterns were predominantly dictated by numerically dominant ant species, as non-numerically dominant ants exhibited predominantly catemeral foraging behaviour both in primary and secondary forests. This was especially prominent in arboreal and semiarboreal dwelling ant communities living in harsh environments of the forest canopies. Nonetheless, whether such variations in diel foraging within ant communities were induced by extreme environmental conditions or interspecific competition is unknown and remains to be investigated. Overall, our study contributes to a better understanding of the ecological mechanisms underlying ant foraging patterns in tropical rainforests, which may have broader implications for the functioning of these complex ecosystems.

4.7. Literature

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4.8. Supplementary Materials

Table S1: List of morphospecies and respective species, subfamilies, and ecological guilds recorded on baits during day and night in tropical rainforests of Papua New Guinea.

	Morphospecies	Species	Subfamily	Guild
1.	ANOC 002	<i>Anochetus</i> sp. 2	<i>Ponerinae</i>	Terrestrial
2.	ANOP 001	<i>Anoplolepis gracilipes</i> (Smith, 1857)	<i>Formicinae</i>	Semi-arboreal
3.	APHA 001	<i>Aphaenogaster</i> sp. aff. <i>dromedaria</i> (Emery, 1900)	<i>Myrmicinae</i>	Terrestrial
4.	CAMP 001	<i>Colobopsis vitrea</i> (Smith, 1860)	<i>Formicinae</i>	Semi-arboreal
5.	CAMP 004	<i>Colobopsis aruensis</i> (Karavaiev, 1933)	<i>Formicinae</i>	Arboreal
6.	CAMP 010	<i>Colobopsis</i> aff. <i>macrocephala</i> (Erichson, 1842)	<i>Formicinae</i>	Arboreal
7.	CAMP 011	<i>Camponotus</i> aff. <i>pictostriatus</i> (Karavaiev, 1933)	<i>Formicinae</i>	Arboreal
8.	CAMP 013	<i>Colobopsis quadriceps</i> (Smith, 1859)	<i>Formicinae</i>	Arboreal
9.	CAMP 016	<i>Camponotus dorycus confusus</i> Emery, 1887	<i>Formicinae</i>	Arboreal
10.	CAMP 018	<i>Camponotus</i> aff. <i>variegatus</i> (Smith, 1858)	<i>Formicinae</i>	Arboreal
11.	CAMP 022	<i>Camponotus anezkae</i> (Klimes & McArthur, 2014)	<i>Formicinae</i>	Arboreal
12.	CAMP 034	<i>Camponotus albocinctus</i> (Ashmead, 1905)	<i>Formicinae</i>	Arboreal
13.	CARD 005	<i>Cardiocondyla</i> aff. <i>. paradoxa</i> (Emery, 1897)	<i>Myrmicinae</i>	Terrestrial
14.	CARE 006	<i>Carebara crassiuscula</i> (Emery, 1900)	<i>Myrmicinae</i>	Terrestrial
15.	CARE 007	<i>Carebara melanocephala</i> (Donisthorpe, 1948)	<i>Myrmicinae</i>	Terrestrial
16.	CARE 009	<i>Carebara</i> sp. 9	<i>Myrmicinae</i>	Terrestrial
17.	CREM 003	<i>Crematogaster polita</i> (Smith, 1865)	<i>Myrmicinae</i>	Arboreal
18.	CREM 004	<i>Crematogaster</i> aff. <i>pythia</i> (Forel, 1915)	<i>Myrmicinae</i>	Arboreal
19.	CREM 011	<i>Crematogaster</i> sp. 11 (Emery, 1901)	<i>Myrmicinae</i>	Arboreal
20.	CREM 015	<i>Crematogaster</i> sp. 15 (Emery, 1897)	<i>Myrmicinae</i>	Arboreal
21.	HYPO 003	<i>Hypoconerina</i> sp. 5	<i>Ponerinae</i>	Terrestrial
22.	IRID 002	<i>Iridomyrmex</i> sp. 1	<i>Dolichoderinae</i>	Terrestrial
23.	LEPM 001	<i>Leptomyrmex fragilis</i> (Smith, 1859)	<i>Dolichoderinae</i>	Terrestrial
24.	MYRM 002	<i>Myrmecina</i> aff. <i>brevicornis</i> (Emery, 1897)	<i>Myrmicinae</i>	Terrestrial
25.	ODON 001	<i>Odontomachus simillimus</i> (Smith, 1858)	<i>Ponerinae</i>	Terrestrial
26.	ODON 003	<i>Odontomachus papuanus</i> (Emery, 1887)	<i>Ponerinae</i>	Terrestrial
27.	OECO 001	<i>Oecophylla smaragdina</i> (Fabricius, 1775)	<i>Formicinae</i>	Arboreal
28.	PACH 001	<i>Ectomomyrmex acutus</i> (Emery, 1900)	<i>Ponerinae</i>	Terrestrial
29.	PAPY 001	<i>Papyrius nitidus</i> (Mayr, 1862)	<i>Dolichoderinae</i>	Terrestrial
30.	PARA 005	<i>Nylanderia</i> aff. <i>vaga</i> (Forel, 1901)	<i>Formicinae</i>	Semi-arboreal
31.	PARA 007	<i>Nylanderia nuggeti</i> (Donisthorpe, 1941)	<i>Formicinae</i>	Terrestrial

32.	PHEI 001	<i>Pheidole</i> sp. 1	<i>Myrmicinae</i>	Terrestrial
33.	PHEI 003	<i>Pheidole</i> sp. 2 aff. <i>sexspinosa biroi</i> (Emery, 1900)	<i>Myrmicinae</i>	Semiarboreal
34.	PHEI 004	<i>Pheidole hospes</i> (Smith, 1865)	<i>Myrmicinae</i>	Semiarboreal
35.	PHEI 005	<i>Pheidole cervicornis</i> (Emery, 1900)	<i>Myrmicinae</i>	Terrestrial
36.	PHEI 007	<i>Pheidole</i> sp. 7	<i>Myrmicinae</i>	Arboreal
37.	PHEI 008	<i>Pheidole laminata</i> (Emery, 1900)	<i>Myrmicinae</i>	Terrestrial
38.	PHEI 010	<i>Pheidole</i> sp. 10	<i>Myrmicinae</i>	Terrestrial
39.	PHEI 011	<i>Pheidole</i> sp. 11 aff. <i>fatigata</i> (Bolton, 1995)	<i>Myrmicinae</i>	Terrestrial
40.	PHEI 013	<i>Pheidole</i> sp. 13 aff. <i>tricolor</i> (Donisthorpe, 1949)	<i>Myrmicinae</i>	Terrestrial
41.	PHEI 014	<i>Pheidole</i> sp. 14 aff. <i>gambogia</i> (Donisthorpe, 1948)	<i>Myrmicinae</i>	Arboreal
42.	PHEI 015	<i>Pheidole</i> sp. 15	<i>Myrmicinae</i>	Terrestrial
43.	PHEI 017	<i>Pheidole</i> sp. 17	<i>Myrmicinae</i>	Terrestrial
44.	PHEI 018	<i>Pheidole</i> aff. <i>distincta</i> (Donisthorpe, 1943)	<i>Myrmicinae</i>	Terrestrial
45.	PHEI 019	<i>Pheidole</i> sp. 19 aff. <i>amplificata</i> (Viehmeyer, 1914)	<i>Myrmicinae</i>	Terrestrial
46.	PHEI 024	<i>Pheidole</i> sp. 24 aff. <i>amber</i> (Donisthorpe, 1941)	<i>Myrmicinae</i>	Arboreal
47.	PHEI 025	<i>Pheidole</i> sp. 25 aff. <i>sexspinosa biroi</i> (Emery, 1900)	<i>Myrmicinae</i>	Semiarboreal
48.	PHEI 027	<i>Pheidole umbonata</i> (Mayr, 1870)	<i>Myrmicinae</i>	Terrestrial
49.	PHEI 086	<i>Pheidole</i> sp. 86	<i>Myrmicinae</i>	Terrestrial
50.	PHEI 087	<i>Pheidole</i> sp. 87	<i>Myrmicinae</i>	Terrestrial
51.	PHEI 088	<i>Pheidole</i> sp. 87	<i>Myrmicinae</i>	Terrestrial
52.	PHIL 001	<i>Philidris</i> aff. <i>cordata</i> (Smith, 1859)	<i>Dolichoderinae</i>	Arboreal
53.	PODO 007	<i>Podomyrma laevifrons</i> (Smith, 1859)	<i>Myrmicinae</i>	Arboreal
54.	POLY 006	<i>Polyrhachis bubastes</i> (Smith, 1863)	<i>Formicinae</i>	Arboreal
55.	POLY 015	<i>Polyrhachis waigeuensis</i> (Donisthorpe, 1943)	<i>Formicinae</i>	Arboreal
56.	POLY 055	<i>Polyrhachis</i> sp. 55	<i>Formicinae</i>	Arboreal
57.	POLY 066	<i>Polyrhachis</i> sp. 66	<i>Formicinae</i>	Arboreal
58.	POLY 067	<i>Polyrhachis</i> sp. 67	<i>Formicinae</i>	Arboreal
59.	POLY 068	<i>Polyrhachis</i> sp. 68	<i>Formicinae</i>	Arboreal
60.	PSEU 001	<i>Pseudolasius</i> aff. <i>breviceps</i> (Emery, 1887)	<i>Formicinae</i>	Semiarboreal
61.	RHYT 001	<i>Rhytidoponera aenescens</i> (Emery, 1900)	<i>Ectatomminae</i>	Terrestrial
62.	RHYT 002	<i>Rhytidoponera strigosa</i> (Emery, 1887)	<i>Ectatomminae</i>	Terrestrial
63.	RHYT 003	<i>Rhytidoponera inops</i> (Emery, 1900)	<i>Ectatomminae</i>	Terrestrial
64.	SOLE 004	<i>Solenopsis papuana</i> (Emery, 1900)	<i>Myrmicinae</i>	Arboreal
65.	SOLE 006	<i>Solenopsis geminata</i> (Fabricius 1804)	<i>Myrmicinae</i>	Terrestrial
66.	STRU 001	<i>Strumigenys</i> aff. <i>loriae</i> (Emery, 1897)	<i>Myrmicinae</i>	Terrestrial
67.	TAPI 001	<i>Tapinoma melanocephalum</i> (Fabricius, 1793)	<i>Dolichoderinae</i>	Semiarboreal

68.	TECH 002	<i>Technomyrmex albipes</i> (Smith F., 1861)	<i>Dolichoderinae</i>	Semiarboreal
69.	TECH 005	<i>Technomyrmex gilvus</i> (Donisthorpe, 1941)	<i>Dolichoderinae</i>	Arboreal
70.	TETR 001	<i>Tetramorium</i> sp. 1	<i>Myrmicinae</i>	Terrestrial
71.	TETR 002	<i>Tetramorium kydelphon</i> (Bolton, 1979)	<i>Myrmicinae</i>	Arboreal
72.	TETR 003	<i>Tetramorium</i> aff. <i>validisculum</i> (Emery, 1897)	<i>Myrmicinae</i>	Semiarboreal
73.	TETR 010	<i>Tetramorium bicolor</i> (Viehmeyer, 1914)	<i>Myrmicinae</i>	Arboreal
74.	VOLL 017	<i>Vollenhovia brachycera</i> (Emery, 1897)	<i>Myrmicinae</i>	Arboreal
75.	WASM 001	<i>Wasmania auropunctata</i> (Roger, 1863)	<i>Myrmicinae</i>	Semiarboreal

Notes: aff represents abbreviation for “affinis“ meaning “related to“.

Table S2: Results of the non-parametric post hoc Tukey HSD tests of interaction between time (day, night) with vertical foraging niche (arboreal, semiarboreal, terrestrial) and interaction between time (day, night) and forest types (primary forests, secondary forests) on the foraging activity (abundance) of the whole ant community and non-numerically dominant ant community recorded on baits.

Predictors	β	SE	Z value	P value
<i>The Whole Ant Community</i>				
Night: Arboreal – Day: Arboreal	-1.433	0.368	-3.893	<u>0.001</u>
Night: Semiarboreal – Day: Semiarboreal	-0.421	0.235	-0.235	0.464
Night: Terrestrial – Day: Terrestrial	-0.254	0.253	-1.005	0.912
Night: Primary – Day: Primary	-0.302	0.246	-1.231	0.606
Night: Secondary: Day: Secondary	-0.757	0.216	-3.512	0.091
<i>Non-Numerically Dominant Ant Community</i>				
Night: Arboreal – Day: Arboreal	-0.186	0.194	-0.960	0.904
Night: Semiarboreal – Day: Semiarboreal	-0.044	0.189	-0.235	0.999
Night: Terrestrial – Day: Terrestrial	-0.232	0.179	-1.292	0.730
Night: Primary – Day: Primary	-0.411	0.234	-1.756	0.291
Night: Secondary: Day: Secondary	-0.070	0.265	-0.250	0.994

Notes: SE represents standard error; P is the type I error probability estimate, β represents regression coefficients.

Table S3: Results of the non-parametric post hoc Tukey HSD tests of the interaction between time (day, night) with vertical foraging niche (arboreal, semiarboreal, terrestrial) and forest types (primary forests, secondary forests) on the foraging activity (abundance) of the whole ant community. The results are presented for a particular type of forest at different time of the day (A), as well as for the same type of the forest at same time of the day (B).

	Predictors	β	SE	Z value	P value
A	Night: Arboreal: Primary – Day: Arboreal: Primary	-1.641	0.478	- 3.433	<u>0.028</u>
	Night: Semiarboreal: Primary – Day: Semiarboreal: Primary	0.504	0.458	1.100	0.994
	Night: Terrestrial: Primary – Day: Terrestrial: Primary	-0.196	0.341	-0.576	1.000
	Night: Arboreal: Secondary – Day: Arboreal: Secondary	-1.364	0.597	-2.284	0.470
	Night: Semiarboreal: Secondary – Day: Semiarboreal: Secondary	-0.726	0.271	-2.685	0.221
	Night: Terrestrial: Secondary – Day: Terrestrial: Secondary	-0.164	0.384	-0.427	1.000
B	Day: Arboreal. Secondary – Day: Arboreal. Primary	0.374	0.553	0.675	0.999
	Night. Arboreal. Secondary – Night: Arboreal: Primary	0.650	0.536	1.213	0.987
	Day. Semiarboreal. Secondary – Day: Semiarboreal: Primary	1.127	0.395	2.856	1.000
	Night. Semiarboreal. Secondary – Night: Semiarboreal: Primary	-0.103	0.368	-1.016	0.997
	Day: Terrestrial: Secondary – Day: Terrestrial: Primary	-0.379	0.373	-1.016	0.997
	Night: Terrestrial: Secondary – Night: Terrestrial: Primary	-0.346	0.362	-0.958	0.998

Notes: SE represents standard error; P is the type I error probability estimate, β represents regression coefficients.

Table S4: Results of the non-parametric post hoc Tukey HSD tests of interaction between time (day, night) with vertical foraging niche (arboreal, semiarboreal, terrestrial) and the forest types (primary forests, secondary forests) on the foraging activity (abundance) of the non-numerically dominant ants. The results are presented for a same type of forest at different time of the day (A), as well as for the different type of the forest at same time of the day (B).

	Predictors	β	SE	Z value	P value
A	Night: Arboreal: Primary – Day: Arboreal: Primary	0.003	0.270	0.010	1.000
	Night: Semiarboreal: Primary – Day: Semiarboreal: Primary	-0.901	0.266	-3.382	<u>0.019</u>
	Night: Terrestrial: Primary – Day: Terrestrial: Primary	-0.310	0.251	-1.237	0.969
	Night: Arboreal: Secondary – Day: Arboreal: Secondary	-0.453	0.336	-1.351	0.943
	Night: Semiarboreal: Secondary – Day: Semiarboreal: Secondary	0.769	0.294	2.616	0.177
	Night: Terrestrial: Secondary – Day: Terrestrial: Secondary	-0.183	0.280	-0.656	0.999
B	Day: Arboreal: Secondary – Day: Arboreal: Primary	0.374	0.553	0.675	0.999
	Night: Arboreal: Secondary – Night: Arboreal: Primary	0.650	0.536	1.213	0.986
	Day: Semiarboreal: Secondary – Day: Semiarboreal: Primary	1.127	0.395	2.856	1.000
	Night: Semiarboreal: Secondary – Night: Semiarboreal: Primary	-0.103	0.368	-1.016	0.997
	Day: Terrestrial: Secondary – Day: Terrestrial: Primary	-0.379	0.373	-1.016	0.997
	Night: Terrestrial: Secondary – Night: Terrestrial: Primary	-0.346	0.362	-0.958	0.998

Notes: SE represents standard error; P is the type I error probability estimate, β represents regression coefficients

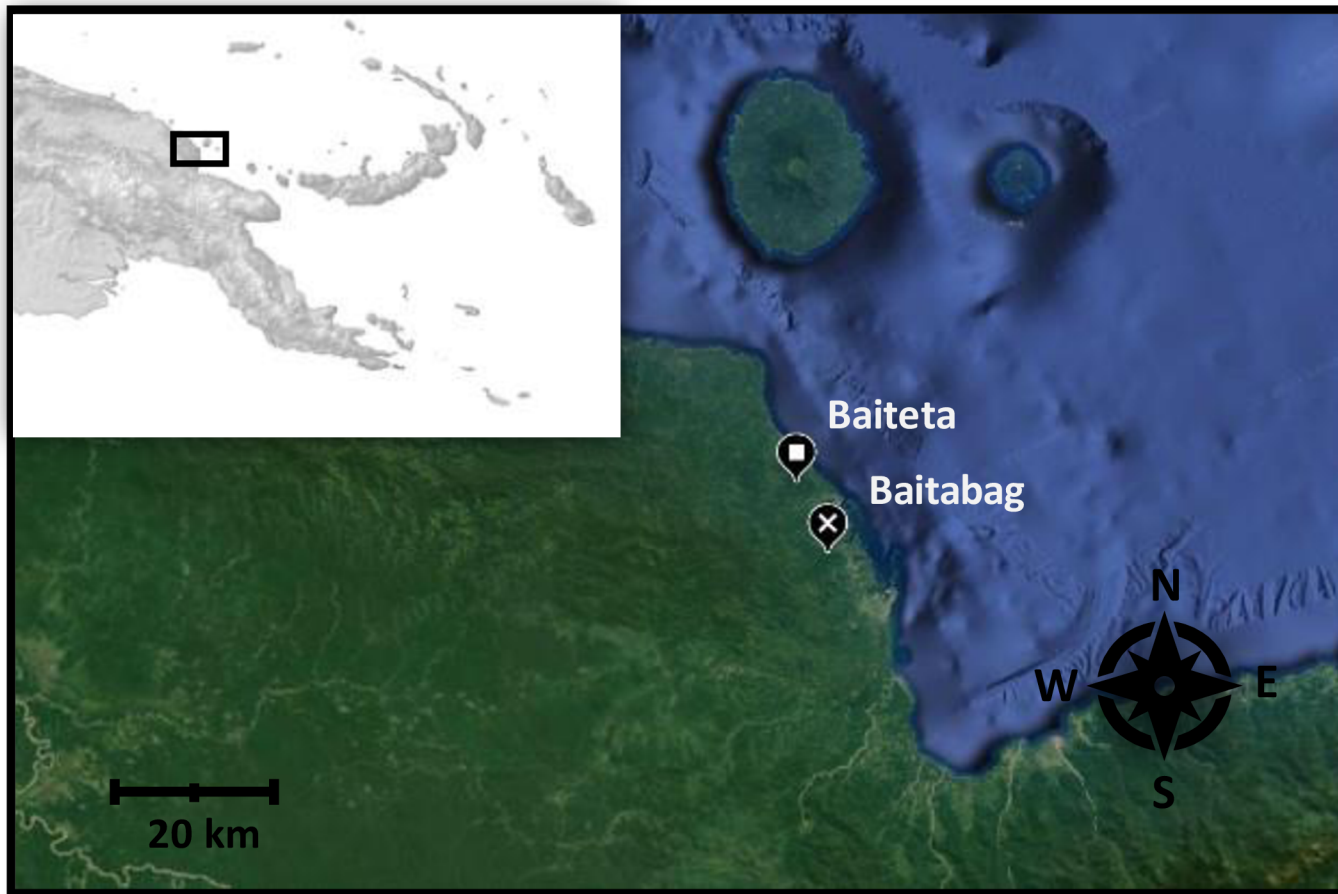


Figure S1: The map of two experimental sites Baiteta and Baitabag ($5^{\circ}01.73'S$, $145^{\circ}46.01'E$, 40 - 80 m. a.s.l, 1200 ha; $5^{\circ}07.99'S$, $145^{\circ}45.47'E$, 40-80 m. a.s.l, 600 ha respectively) located in Madang Province, Papua New Guinea.

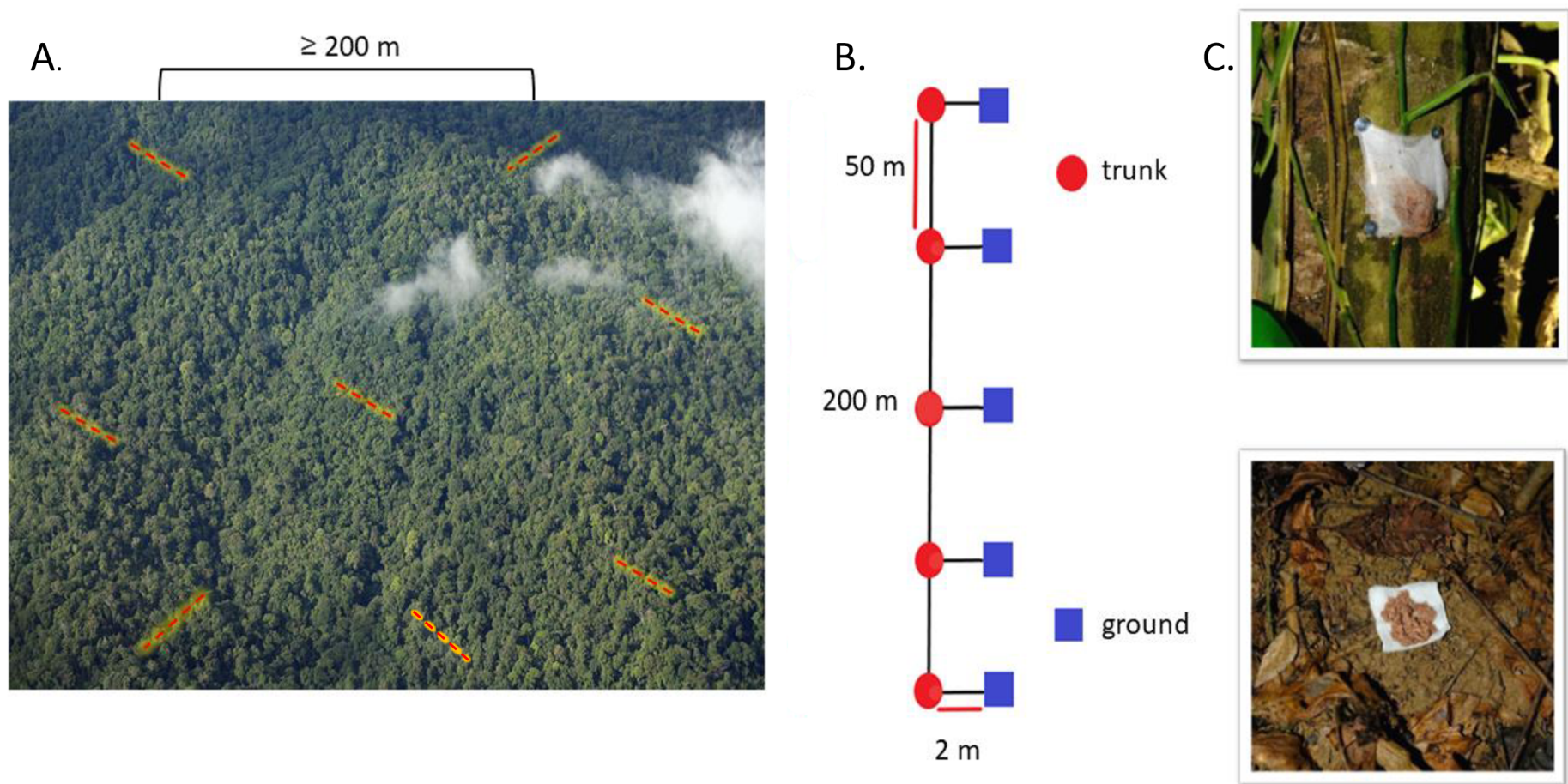


Figure S2: Illustration of the methodology used in the study to survey day/night ant communities in tropical rainforests in Papua New Guinea. The figure consists of three panels. Panel (A) shows the distribution of eight transects across the rainforest. Panel (B) shows a schematic transect used in the study. Panel (C) shows the baits used in the study (the ground bait shown in the panel is for illustration only, all baits were set under the first layer of the gauze without exception).

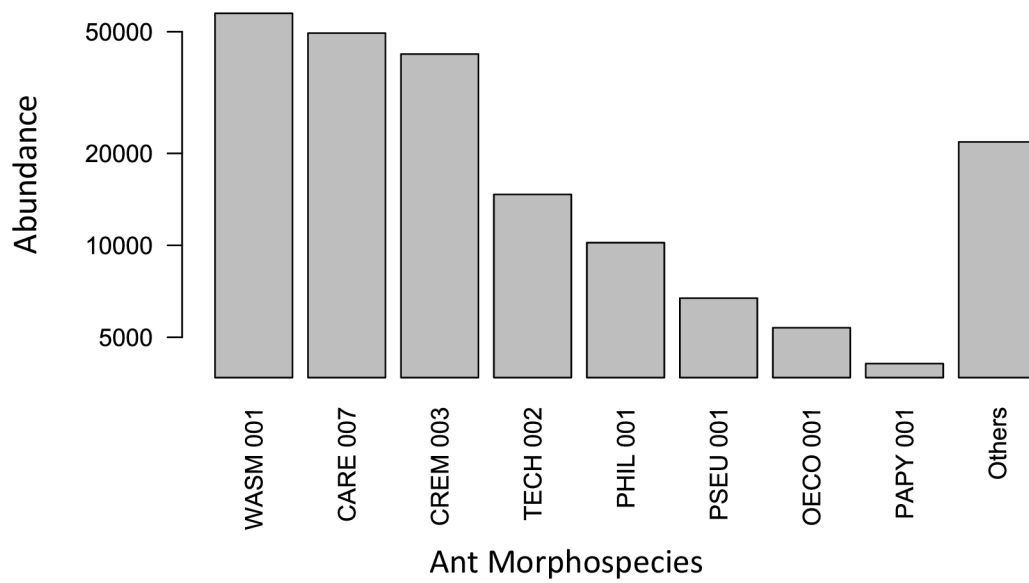


Figure S3: The bar plot representing recorded/estimated ant abundance on baits of eight numerically dominant ant morphospecies which account for 90% of the total ant abundance (Wasm 001, Care 007, Crem 003, Tech 002, Phil 001, Pseu 001, Oeco 001, Papy 001) and the rest of the ant community (67 ant morphospecies) accounting for the remaining 10% (Others). For more information about individual ant morphospecies (species, subfamily, guild) see Table S1.