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Ant assemblage composition explains high predation pressure on artificial caterpillars during early night

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Abstract. 1. Predator–prey interactions, especially those involving herbivorous insects, are of great importance in maintaining biodiversity. Predation pressure varies temporally in response to prey availability and activity. However, little is known about the patterns and drivers of fluctuations in predation pressure at fine temporal scales.

2. Artificial caterpillars (placed on plant leaves at breast height) were used to assess changes in predation pressure across four time intervals of the day in a monsoonal tropical rainforest in south-west China. The study examined how assemblage composition of arboreal ants, the dominant predators, changed across the same time intervals. The potential linkages between biotic (arboreal ants) and abiotic (temperature and light intensity) factors with predation rate were evaluated.

3. Predation rate on caterpillars during the early part of the night (19.00–01.00 hours) was significantly higher than in the morning, afternoon, or late night. Ant assemblage composition, rather than species richness or total abundance, best explained the variations in predation rate on artificial caterpillars.

4. The results help to strengthen understanding of trophic interactions by demonstrating that predation pressure fluctuates at finer timescales than previously tested, and that a particular set of ant species may play major roles in predation on caterpillars and possibly other organisms.

Key words. β diversity, diel timescale, Formicidae, predator–prey interactions, species interactions.

Introduction

Predation is one of the most important and common biological interactions in both terrestrial and marine ecosystems across latitude, longitude and elevation (Taylor, 2013; Roslin *et al.*, 2017), which contributes to the formation and maintenance of biodiversity (Chesson,2000) and ecosystem functions and services (Worm *et al.*, 2006; Mougi & Kondoh, 2012). Predator–prey interactions can drive the evolution of traits for both prey and predator, and affect speciation and extinction (Jablonski, 2008). Predators can shape morphological and chemical defence traits (Greeney *et al.*, 2012) and biological rhythms of prey (Heinrich, 1979). In response to prey availability and activity, predation pressure varies across different timescales, including diel, lunar, seasonal and annual

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cycles (Lima & Bednekoff, 1999; Ferrari *et al.*, 2008; Ferrante *et al.*, 2017).

Diel (i.e. within-day) variability of predation pressure has been studied in several vertebrate systems. Examples include common rabbit (*Oryctolagus cuniculus*) and mammalian mesopredators in southern Europe (Monterroso *et al.*, 2013), and wolves (*Canis lupus*) and moose (*Alces alces*) in North American boreal forest (Vander-Vennen, 2014). Among invertebrates, lepidopteran larvae have been the subject of several empirical and theoretical studies that investigated temporal variability of their predation rate (Heinrich, 1979; Seifert *et al.*, 2016; Ferrante *et al.*, 2017). Lepidopteran caterpillars (hereafter 'caterpillars') mostly forage during the night to avoid the activity peak of their predators (e.g. ants, birds and wasps) (Bernays, 1997). Seifert *et al.* (2016) found that the predation rate on artificial caterpillars in an Amazonian primary lowland rainforest was higher during the daytime (06.15–18.15 hours) than at night (18.15–06.15 hours), which was consistent with previous predictions (Heinrich, 1979). However, in a temperate forest, Ferrante *et al.* (2017) found that predation rate at night was higher than during the day. Diel variability of predation pressure is still under debate, and potential drivers of such patterns are poorly understood.

Ants are important predators of caterpillars, especially in the tropics (Roslin *et al.*, 2017). Accumulated evidence indicates temporal variability in ant assemblage composition (e.g. Lindsey & Skinner, 2001; Dáttilo *et al.*, 2014; Yusah *et al.*, 2018), which may in turn affect the temporal variability of predation rate. Levels of foraging intensity (and hence predation pressure) may be different among ant species so that predation pressure may change if different sets of ant species are found across different times of the day. However, we know little about the potential linkages between temporal variability of predation pressure and ant assemblages.

Ant assemblage composition, abundance, and species richness could affect predation rate through top-down effects (Dyer *et al.*, 2004). Based on prey-offering experiments in the tropical lowland rainforest in Malaysia, Floren *et al.* (2002) found that 46 out of 54 ant species were predators of caterpillars, while the other eight ant species were not. This suggests that, in addition to abundance of ants, the composition and richness of ant assemblages are likely to affect the predation pressure (Harvey & Eubanks, 2004; Styrsky *et al.*, 2006), while the counter-examples exist (Tiede *et al.*, 2017). However, few studies have quantified the relative importance of ant assemblage composition, abundance, and species richness on predation pressure.

Here we propose two alternative (but not mutually exclusive) hypotheses to explain how activities of various ant species may affect predation rate on caterpillars. First, the 'temporal generalist hypothesis' that the majority of predatory ant species occupy continuous temporal niches and forage throughout the day and night, so that predation pressure is similar across different times of the day. According to the second, the 'temporal specialist hypothesis', predatory ants occupy discrete temporal niches and forage at different times of the day, causing variable predation pressure across different times of the day.

Assessing predation rate based on artificial caterpillars made of odourless and non-toxic coloured plasticine is a simple measure of predation pressure, and has been widely employed (e.g. Posa *et al.*, 2007; Howe *et al.*, 2009; Tvardikova & Novotny 2012; Ferrante *et al.*, 2014, 2017; Low *et al.*, 2014; Lövei & Ferrante, 2017; Roslin *et al.*, 2017). Here we used artificial caterpillars exposed on plant leaves in a natural rainforest at Xishuangbanna Tropical Botanical Garden, Yunnan Province, southwest China, to study the diel variability of predation rate on caterpillars. Specifically, we assessed the following questions: (i) does the predation rate on artificial caterpillars peak at a particular time interval; (ii) can the temporal generalist or the temporal specialist hypotheses explain the patterns of temporal changes in predation pressure; and (iii) which of the biotic (ant abundance, species richness, and assemblage composition) and abiotic drivers (temperature and light intensity) best explain the temporal variation in predation pressure on artificial caterpillars?

Materials and methods

Study area

This study was conducted in the Xishuangbanna Tropical Botanical Garden (XTBG), Menglun, Xishuangbanna Dai Autonomous Prefecture, Yunnan Province, southwest China (101°25′E, 21°41′N, 570 m asl). The XTBG receives a mean annual precipitation of 1557 mm, with most of the precipitation (83%) occurring during the wet season (May to October). Mean annual temperature is 21.5 °C, with the monthly average ranging from 15.2 (January) to 24.6 °C (July) (Zhu, 1992; Zhu *et al.*, 2015). The original native vegetation is monsoonal tropical rainforest, but much is fragmented today because of rubber tree (*Hevea brasiliensis*) plantations and infrastructure construction.

Experimental design

We selected a protected rainforest in XTBG and delineated an 800-m × 1000-m area as our study location. The predation experiment was conducted in November 2017, during the early dry season. We avoided the rainy season (April to October) to minimise the impacts of frequent rainfall on the predation experiment. We established four study sites (blocks) at least 150 m away from each other. Each site included four 5-m × 10-m plots for the predation experiment and another four 5-m × 5-m plots for ant sampling, with 10-m buffer zones between the plots (Fig. S1), resulting in a total of 32 plots. Our experiment had a randomised block design with time interval as main treatment factor. Plots at each site were randomly allocated to one of the four temporal intervals covering 6 h consecutively for caterpillar deployment and ant trapping: 07.00–13.00 hours (morning), 13.00–19.00 hours (afternoon), 19.00–01.00 hours (early night), and 01.00–07.00 hours (late night). These temporal intervals were set according to the sunset and sunrise times in mid-November (07.25 and 18.36 hours, respectively). We retrieved all the caterpillars (i.e. both predated and untouched caterpillars) after a 6-h exposure, and we only used each experimental site once (i.e. for 24 h); hence no caterpillars or experimental sites were reused. This was done to avoid predators learning to return to (or avoid) the experimental caterpillars at the same position, as suggested by Lövei & Ferrante (2017). We conducted our study at four sites on separate days (7–8, 10–11, 12–13, and 14–15 November). In addition, temperature and light intensity were measured in each plot during the corresponding time intervals using a HOBO Pendant Temperature/Light Data Logger (Onset Computer Corporation, Bourne, MA, U.S.A.), which was hung on a tree branch *c.* 1.2 m above the ground.

Artificial caterpillar setup and control

The artificial caterpillars were made from an equal mixture of green and light green plasticine (Newclay Products Ltd, Newton Abbot, U.K.), which is oil-based and non-toxic, to represent geometrid larvae, following the methods proposed by Roslin *et al.*, (2017). Although non-geometrid moths are also commonly found in this area, we opted to use caterpillars representing geometrids, as this family is commonly found elsewhere and used in many studies to quantify predation pressure (Lövei & Ferrante, 2017). The caterpillars with smooth round shape (diameter 3 mm, length 30 mm) were modelled using a metal syringe. We transported the caterpillars to the field in 2-ml plastic Eppendorf (Hamburg, Germany) tubes, to avoid any undesired marks during transportation. For every plot (5 m × 10 m), we set 50–55 artificial caterpillars on plant leaves at 0.5–1.5 m above ground. Artificial caterpillars were bent to mimic real geometric larvae, and pinned to plant leaves. We used pins instead of glue to fix caterpillars, as pinning was much quicker than gluing, and glued plasticine larvae often fall after rainfall. The caterpillars were set *c.* 1 m apart from each other (Fig. S1). We acknowledge that this distance does not make the caterpillars fully independent. Statistical analysis was therefore conducted by either calculating predation rate per plot or using individual caterpillars whilst controlling for the effects of non-independence (i.e. site effects) (see more details in the following). A total of more than 800 caterpillars were used for the entire experiment (50–55 caterpillars × four plots × four sites = over 800 caterpillars).

We collected the caterpillars after 6 h and transported them in 5-ml plastic Eppendorf tubes to the laboratory (the larger tubes were used to minimise undesired damage after exposure). Marks of predation were checked with magnifying glass and dissecting microscope following recommended practice (Howe *et al.*, 2009; Tvardikova & Novotny, 2012; Low *et al.*, 2014; Sam *et al.*, 2015, 2016; Roslin *et al.*, 2017). We identified signs of four predator groups (ants, other invertebrates, birds and uncertain) based on characteristic attack marks (Table S1). We excluded the missing caterpillars (74 out of 876 caterpillars deployed) from analysis.

Ant sampling and identification

At the same time that artificial caterpillars were set, we set 10 baited arboreal pitfall traps (plastic tubes, diameter 45 mm, depth 55 mm) in nearby plots. We used plastic tape to fix the traps on tree stems at a height of 0.5–1.5 m, to be consistent with the height of artificial caterpillars. Traps were set at least 1 m away from each other. A mixture of honey, peanut butter and sardine oil was applied to the inner wall of traps, which were then partially filled with 50% ethanol (Lawes *et al.*, 2017). Traps were run for 6 h (the same duration as the artificial caterpillar experiment in each plot). All ants collected were identified to genus, and then species or morphospecies.

Statistical analysis

We conducted all statistical analyses using R v.2.15.1 (R Core Team, 2015).

Predation rate. We first examined the differences in predation rate between day and night, and among the four different time intervals. To calculate the predation rate during the day and night, we pooled two plots which were run at 07.00–13.00 hours (morning) and 13.00–19.00 hours (afternoon) for the day, and 19.00–01.00 hours (early night) and 01.00–07.00 hours (late night) for the night. Predation rate was calculated by dividing the number of predated caterpillars by the total number of caterpillars retrieved from each treatment (plot) per site. One caterpillar during the early night was predated by both ants and non-ant predators and they were treated as two separate predations when predations by ants and non-ants were analysed individually. We conducted ANOVA with site as a random factor to test the differences among the time intervals, and employed Tukey's honestly significant difference (HSD) test with site as random effect for multiple comparisons at the $P < 0.05$ level to evaluate the pairwise differences using the '`glht`' function in the `multcomp` package (Hothorn *et al.*, 2014; R Core Team, 2015).

We tested the relationship between environmental factors (temperature and light intensity) and predation rate using simple linear models with the '`lm`' function. We calculated Akaike's information criterion corrected for small sample sizes (AICc) using the '`AICc`' function to evaluate relative support for each linear model we built. We used the information-theoretic evidence ratio [ER, *w*AICc (candidate model): *w*AICc (intercept-only null model)] as an index of relative support for the linear slope model versus the null model; when ER > 1.5, we deemed that there was evidence to support the candidate model (Burnham *et al.*, 2011; Liu *et al.*, 2017).

Ant assemblages. We calculated species richness, total abundance, and Shannon's evenness for ant assemblages in each plot using the '`diversity`' function in the `vegan` package (Oksanen *et al.*, 2013). We tested the differences in these diversity indices among the four different time intervals using ANOVA and Tukey's HSD. We also employed correspondence analysis (CA) to test the associations between predation by ants and ant assemblage composition (presence/absence data) using the first and second axes of the CA. Strength and direction of the relationship were presented as a vector, and we ran 9999 permutations of the

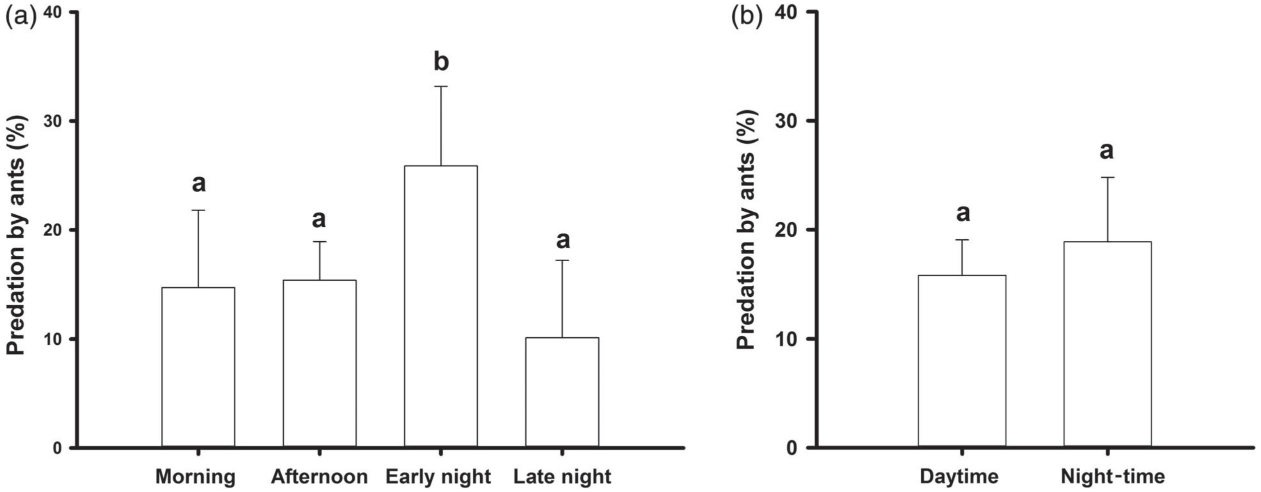

Fig. 1. Predation by ants across four different time intervals (a) and day- and night-time intervals (B). Different letters indicate statistically significant differences among the different time intervals based on Tukey's honestly significant difference test for multiple comparisons at the $P < 0.05$ level. Time intervals in (a) are: morning (07.00–13.00 hours); afternoon (13.00–19.00 hours); early night (19.00–01.00 hours); and late night (01.00–07.00 hours). The time intervals in (b) are: daytime (07.00–19.00 hours) and night-time (19.00–07.00 hours). Data are means + SE.

samples (plots) to obtain a null distribution of pseudo-*F* ratios; statistical significance was then assessed by the rank of observed pseudo-*F* ratio (Anderson & Walsh, 2013). We employed permutational multivariate analysis of variance (PERMANOVA) to test the effects of study site and time interval on ant assemblage composition (based on Jaccard distance) using the '`adonis`' function. The overall procedure was run for 9999 permutations to assess statistical significance.

We compared β diversity of ant assemblages between time intervals based on Jaccard and Bray–Curtis distance matrices, using the '`vegdist`' function. We used the '`randomizeMatrix`' function in the `picante` package (Kembel *et al.*, 2010) with the 'independent swap' method to obtain a null distribution of Jaccard and Bray–Curtis indices based on 9999 permutations. We considered that β diversity was significantly different from the null model when the 95% CIs of the observed Jaccard and Bray–Curtis indices did not include means of the null model values. We also investigated how many ant species were specific to certain time intervals.

Relationship between predation by ants and ant assemblage. We used simple linear models (using the '`lm`' function) to test the relationships between predation by ants and various diversity indices of ant assemblages. These included species richness, total abundance, Shannon's evenness, and the first axis value of correspondence analysis (hereafter 'CA1'). We calculated the AICc, ER, and *w*AICc. We also calculated the percentage deviance explained in the response variable (De) as an index of each model's goodness-of-fit (Burnham *et al.*, 2011).

We employed an information theory approach to further test what factors (time interval, CA1, or both) best explained predation by ants. To this end, we treated individual artificial caterpillars as the response variable (i.e. binomial incidence of predation by ants per caterpillar), and treated time interval and CA1 as the independent variables in generalised linear mixed-effects models using the `lme4` package. We set the site as a random effect and validated the use of a binomial family with 'logit' link for the modelled error distribution. As a measure of the model's goodness-of-fit (Schielzeth & Nakagawa, 2013), we calculated AICc and likelihood-ratio-based pseudo-R^2 values for all candidate models. The pseudo-R^2 was calculated using the '`r.squaredLR`' function in the `mumin` package.

Results

Predation rate

Out of a total of 876 caterpillars deployed, we recovered 802 caterpillars and observed 145 predated caterpillars, of which 132 (91%) were predated by ants, and additional five caterpillars (3%) were predated by other invertebrates (Table S1). Additionally, three bird predation events were observed; two of them occurred during the afternoon, and one occurred during the early night. So the total average predation rate of dummy caterpillars was 18% after 6 h exposure. A total of 74 out of 876 (8.4%) caterpillars were lost. We found no significant effect of time interval on the number of caterpillars lost (ANOVA, $F_{3,12} = 1.085$, $P = 0.393$). The effect of time interval was marginally significant on predation by ants ($F_{3,12} = 3.083$, $P = 0.068$). *Post hoc* tests showed that predation by ants during the early night (19.00–01.00 hours) was significantly higher than during the other three time intervals (Fig. 1). Although not significant, we recorded the lowest predation by ants during the late night. When time intervals were pooled into day and night only, we found no significant differences in predation by ants (Fig. 1) (ANOVA, $F_{1,6} = 4.055$, $P = 0.091$). The total predation rate (i.e. ants plus other predators) showed the same trend with predation by ants. Despite the significant differences among the four time intervals, we found no relationship between predation by

Table 1. . Results of permutational multivariate analysis of variance (PERMANOVA) for the effects of time interval and study site (block) on Jaccard and Bray–Curtis distance measures of ant assemblages, showing the degrees of freedom (d.f.), F statistic, partial R^2 and P-value.

Term	d.f.	F	Partial R^2	P
Jaccard distance				
Time interval	3	1.213	0.211	0.067
Site	3	1.865	0.325	<0.001
Residuals	8		0.464	
Bray–Curtis distance				
Time interval	3	1.354	0.211	0.051
Site	3	2.396	0.373	<0.001
Residuals	8		0.416	

ants and environmental factors (temperature and light intensity) (Fig. S2).

Ant assemblages

We collected 27 ant species in 13 genera from our 16 plots. We found no significant differences of ant species richness (ANOVA, $F_{3,12} = 0.588$, $P = 0.638$), total abundance ($F_{3,12} = 1.132$, $P = 0.387$), and Shannon's evenness ($F_{3,12} = 1.016$, $P = 0.430$) among the four different time intervals (Fig. S3). There were strongly significant site differences ($P < 0.001$) on ant assemblage composition for both Jaccard and Bray–Curtis indices, whereas we found a weaker effect of time interval ($P = 0.067$ and 0.051 for Jaccard and Bray–Curtis indices, respectively; Table 1).

Values of β diversity between the early and late night, and also between early night andafternoon, were significantly higher than the null model values regardless of the index used (Fig. S4). This suggested significantly high dissimilarity in ant assemblage composition between early and late night, and between early night and afternoon. In addition, only one and two ant species' occurrences were restricted to the morning and afternoon, respectively. By contrast, four species were restricted to occur during the early night and nine during the late night (Table 2).

Relationship between predation by ants and ant assemblage composition

We found no relationship between predation by ants and total abundance (ER = 0.23, De = 0.01), species richness (ER = 0.25, De = 0.02), or Shannon's evenness (ER = 0.24, De = 0.01) (Fig. S5). However, we found a strong linear relationship between predation by ants and CA1 (AICc = −24.70, ER = 2.59, De = 0.29) (Fig. 2). Similarly, CA showed that predation by ants was significantly associated with ant assemblage composition ($R^2 = 43.06$, $P = 0.033$) (Fig. S6). Using generalised linear mixed-effects models, we found that the combination of time interval and CA1 (AICc = 661.84, wAICc = 1.000, pseudo-$R^2 = 0.140$) was the most parsimonious model explaining the variation in predation pressure (by ants) (Table S2).

Table 2. Relative abundance of individual ant species during the four time intervals: morning (07.00–13.00 hours); afternoon (13.00–19.00 hours); early night (19.00–01.00 hours); and late night (01.00–07.00 hours).

Ant species	Morning	Afternoon	Early night	Late night
Camponotus sp. 1*	–	–	–	0.083
Carebara sp. 1*	–	0.144	–	–
Crematogaster sp. 1	–	0.063	0.103	0.083
Crematogaster sp. 2	0.152	0.007	–	0.103
Gnamptogenys sp. 1*	–	–	0.375	–
Monomorium sp. 1*	–	–	–	0.014
Monomorium sp. 2*	–	–	–	0.130
Monomorium sp. 3	0.009	0.250	–	–
Monomorium sp. 4*	–	–	–	0.010
Monomorium sp. 5*	–	–	–	0.010
Nylanderia sp. 1	0.048	0.010	–	0.030
Nylanderia sp. 2	0.269	0.003	0.015	0.021
Nylanderia sp. 3*	–	0.003	–	–
Nylanderia sp. 4	–	0.005	–	0.010
Odontoponera sp. 1	0.056	0.005	–	–
Pheidole sp. 1	0.246	0.225	–	0.256
Pheidole sp. 2	0.188	0.242	–	–
Polyrhachis sp. 1*	–	–	0.081	–
Polyrhachis sp. 2*	–	–	–	0.052
Polyrhachis sp. 3*	–	–	0.022	–
Recurvidris sp. 1*	–	–	–	0.094
Strumigenys sp. 1*	–	–	–	0.010
Technomyrmex sp. 1	0.009	–	0.037	–
Technomyrmex sp. 2	0.019	0.045	0.103	0.083
Tetramorium sp. 1*	0.004	–	–	–
Tetramorium sp. 2*	–	–	0.015	–
Tetramorium sp. 3*	–	–	–	0.010

*, ant species occurrence restricted to a certain time interval.

Discussion

The total average predation rate in this study (18% after 6 h exposure) was higher than other studies in tropical regions [e.g. 74.6% after 5 days (Sam *et al.*, 2015); 34.5% after 24 h (Seifert *et al.*, 2016); 20.9% after 4 days (Leles *et al.*, 2017)] when we standardise it to predation rate over 24 h exposure (Lövei & Ferrante, 2017). We attributed the relatively high predation rate in our system to: (i) the predation caused by predators which had yet to learn to avoid the artificial caterpillars; and (ii) relatively high predation by ants (91%).

Unlike the previous studies which divided diel time into only day and night (Seifert *et al.*, 2016; Ferrante *et al.*, 2017), our study subdivided diel time into four time intervals (morning, afternoon, early and late night). We found that both total predation rate and predation by ants were highest during the early night (19.00–01.00 hours). We found associations between predation rate and ant assemblage composition, suggesting that a particular set of ant species active during the early night may be more aggressive, potentially contributing to the increased predation rate at this time. Ant species richness, abundance, and abiotic factors (temperature and light intensity) did not explain the observed patterns of predation by ants.

In this study, invertebrates (including ants) accounted for 94% of predation events, which was similar to the previous studies not only in this area (Leles *et al.*, 2017), but also in other

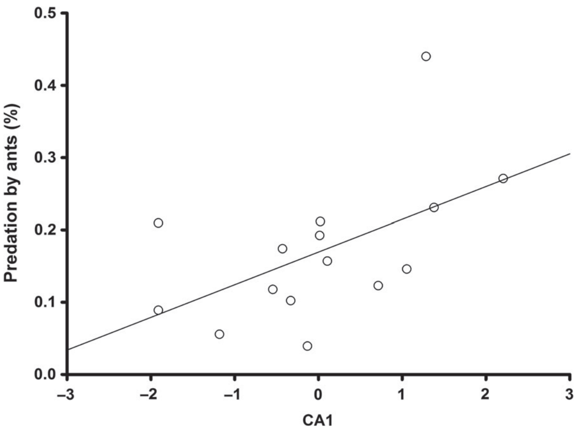

Fig. 2. The relationship between predation by ants and primary correspondence analysis axis value (CA1) based on ant assemblages [Akaike information criterion corrected for small sample sizes (AICc) = −24.70, evidence ratio (ER) = 2.59, percentage deviance explained in the response variable (De) = 0.288]. Note that ER was greater than the threshold value of 1.5.

tropical ecosystems (Loiselle & Farji-Brener, 2002; Sam *et al.*, 2015). We found no significant differences in predation by ants between the day and night, which is consistent with predation by ants found in Amazonian rainforests (Seifert *et al.*, 2016). However, Seifert *et al.* (2016) found that total predation rate (i.e. predation by all predators) was greater during the day than at night, whereas we found no such differences. By contrast, Ferrante *et al.* (2017) found that predation rate at night was higher than during the day and argued that no enemy-free time existed at night for caterpillars. It is important to note that 91% of the predation events we observed in this study were contributed by ants, much higher than in Seifert *et al.* (2016) (49%) or in Ferrante *et al.* (2017) (1.9%). All three bird predation events in our study occurred during the afternoon or early night (13.00–01.00 hours), which was in line with the diurnal rhythm of bird activity (Palmgren, 1949) and consistent with Seifert *et al.* (2016). The relatively low bird predation rate (0.34%) indicated that birds were not a major predator for caterpillars in this study area, at least in the understorey of natural rainforests with high canopy density. This may reflect anthropogenic disturbance, given that these forests are missing many of their understorey birds as a result of hunting (Harrison *et al.*, 2013).

Surprisingly, environmental factors, including temperature and light intensity, did not affect predation rate, which was inconsistent with the general idea that temperature could influence predation rate (Rall *et al.*, 2010; Karban *et al.*, 2015). Temperature is perhaps positively associated with predation rate at larger temporal scales (e.g. inter-annual or seasonal patterns), and across large spatial scales (Tiede *et al.*, 2017). We have two reasons to explain these non-significant results. First, we attribute the non-significant effects to the fact that predation rate was higher in only the first half of the night, and this asymmetrical pattern might obscure the potential effects of temperature and light intensity on predation rate. Second, environmental factors may have a greater impact on predation rate over large spatial and temporal scales. However, at the finer temporal scale employed by our study, we suggest that the effect of predator (mainly ants) assemblage composition played a more important role than environmental factors.

Our results indicate that different ant species dominated different time intervals. This is concordant with several previous studies on temporal dynamics of ants in other ecosystems (Talbot, 1946; McClusky & Neal, 1990; Lindsey & Skinner, 2001; Dáttilo *et al.*, 2014). For instance, Albrecht & Gotelli (2001) found that the two most abundant ant species negatively correlated along the diel timescale in a grassland of Oklahoma, and Lynch *et al.* (1980) also found that three sympatric ant species occupied and dominated the woodland ecosystem during different time intervals. Such temporal niche partitioning could reflect ant species' thermal preference (Lynch *et al.*, 1980), colonisation–competition trade-offs (Holway, 1999), or interspecific competition (Bernstein, 1979; Carothers & Jaksic, 1984; Human & Gordon, 1996; Albrecht & Gotelli, 2001). It is also important to note that ant assemblage composition was influenced not only by time interval but also by study site location, indicating the important role of spatial factors in shaping ant assemblage composition in the monsoonal tropical rainforest (e.g. Mezger & Pfeiffer, 2011; Flores *et al.*, 2018; Yusah *et al.*, 2018).

In our study, ant species' occurrences that were restricted to a certain time interval were found mostly at night, while ant species occupying continuous temporal niches were found during the day (Table 2). Four ant species (*Gnamptogenys* sp.1, *Polyrhachis* sp.1, *Polyrhachis* sp.3, *Tetramorium* sp.2) occurred only during the early night, and we suggest that some of these species might be more aggressive, and potentially contributing to higher predation rate. Together, the temporal generalist hypothesis was mainly applicable during the day (07.00–19.00 hours), as we found that the same set of predatory ant species occurred continuously throughout the day, creating the consistent predation pressure during the morning and afternoon. However, the temporal specialist hypothesis is likely to be applicable at night (19.00–07.00 hours), as we found discrete sets of predatory ants occupying different temporal niches, and showing different predation pressure possibly exerted by different ant species. Ant species differ in efficacy of predation on caterpillars (Floren *et al.*, 2002). For example, Lach *et al.* (2016) found that one ant species, *Anoplolepis gracilipes*, exerted 4.4–16.0 times greater predation rate than other co-occurring ant species of tropical forests. In their study, *A. gracilipes* was considered to be a 'super' predator. Similarly, the four ant species that occurred solely during the early night might be 'super' predators of caterpillars in our system.

However, the potential linkage between ants and caterpillar predation must be considered carefully, for two reasons. First, ant surveys involved baiting, which captured ants by smelling and tasting attraction as opposed to artificial caterpillars, which attract ants by visual cues. Ants sampled by baiting, therefore, may not represent true predators of artificial caterpillars. Further studies with video recordings are needed to confirm the linkages between predation rate and ant assemblage composition. Second, abundance could simply increase the predation rate directly through top-down effects (Pace *et al.*, 1999; Piovia-Scott *et al.*, 2017). However, our results showed that neither ant species richness nor total abundance could explain the variation in predation rate. Despite temporal differences in predation rate, both ant species richness and total abundance were more or less the same across four time intervals.

Overall, our results help to enhance the understanding of trophic interactions along the diel timescale by demonstrating that predation pressure fluctuates at finer timescales than previously considered, and that a particular set of ant species, rather than species richness or abundance *per se*, can drive this pattern.

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Supporting Information

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

Table S1. Number of predated artificial caterpillars recorded at different time intervals.

Table S2. Summary results of generalised linear mixed-effects models for predation by ants as a function of time interval and the first CA axis values of ant assemblages.

Fig. S1. Schematic diagram of a study site.

Fig. S2. Relationships between predation rate by ants and environmental factors (temperature and light intensity).

Fig. S3. Mean ant species richness, Shannon's evenness, and total abundance among the four different time intervals.

Fig. S4. Mean and 95% confidence interval of β diversity indices of ant assemblages between different time intervals.

Fig. S5. Relationships between predation rate by ants and total ant abundance, ant species richness, and ant Shannon's evenness.

Fig. S6. Correspondence analysis (CA) of ant assemblage composition.

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