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Day-Night Dynamics in the Organisation of Ant–Plant Interaction Networks in a Brazilian Amazon Rainforest

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ABSTRACT

Interactions between ants and plants bearing extrafloral nectaries (EFN-bearing plants) represent a classic plant defence strategy that involves a high diversity of species in tropical forests. Several studies have investigated the structuring processes of these ant–plant interactions across spatial and temporal scales. However, surprisingly little is known about how these interactions vary throughout the day. In this study, we investigated daily variations in ant–plant interactions mediated by extrafloral nectaries in a Brazilian tropical forest, using a complex network approach and beta-diversity analysis of interactions. We sampled these ant–plant interactions in nine 150 × 10 m plots over three periods of the day (morning, afternoon and night). We organised the data from each period into quantitative matrices and combined data from two and three periods to investigate possible increases in network descriptors. We calculated the total beta diversity of interactions, as well as its additive components (species turnover and interaction rewiring), across different pairs of periods. We found that network specialisation and nestedness remained constant throughout the day. However, at night, the networks exhibited reductions in network size, the number of interactions and diversity of interactions. Networks combining data from three periods showed pronounced increases in network size and the number of interactions compared with two- and single-period networks, suggesting temporal niche partitioning associated with extrafloral nectaries. Compositional changes were also detected through the beta diversity of interactions. Greater species turnover and interaction rewiring occurred between the nocturnal period and both diurnal periods. Our results underscore the critical role of the daily temporal scale in structuring these mutualistic networks and reveal how distinct ant foraging strategies partition the resource in time, cautioning against ecological interpretations derived solely from diurnal sampling.

RESUMO

Interações entre formigas e plantas portadoras de nectários extraflorais representam uma clássica estratégia de defesa de plantas, que envolve uma elevada diversidade de espécies em florestas tropicais. Diversos estudos têm investigado sobre os processos estruturadores destas interações no espaço e no tempo. No entanto, sabemos relativamente pouco sobre como essas interações mudam ao longo do dia. Neste estudo, investigamos variações diárias nas interações formiga-planta mediadas por nectários extraflorais em uma floresta tropical brasileira, usando uma abordagem de redes complexas e análises de diversidade beta de interações. Amostramos essas interações em nove parcelas de 150 × 10 m em três períodos do dia (manhã, tarde e noite). Organizamos os dados de cada período em matrizes quantitativas e combinamos dados de dois e três períodos para investigar possíveis aumentos nos descritores de rede. Calculamos a diversidade beta total de interações, bem como seus componentes aditivos (substituição de espécies e reconfiguração de interações) entre diferentes pares de períodos. Constatamos que a especialização e o aninhamento das redes permaneceram constantes ao longo do dia. Contudo, à noite, as redes exibiram reduções no tamanho, número de interações e diversidade de interações. Redes com dados combinados de três períodos mostraram aumentos acentuados no tamanho e no número de interações em comparação com redes de dois períodos e de período único, sugerindo uma partição temporal de nicho associada a nectários extraflorais. Mudanças composicionais também foram detectadas por meio da diversidade beta de interações. Uma maior substituição de espécies e religação de interações ocorreu entre o período noturno e ambos os períodos diurnos. Nossos resultados destacam o papel crucial da escala temporal diária na estruturação dessas redes mutualísticas e revelam como diferentes estratégias de forrageamento das formigas dividem o recurso ao longo do tempo, alertando contra interpretações ecológicas derivadas exclusivamente de amostragem diurna.

1 | Introduction

Tropical forests are known for their high biodiversity, especially of arthropod species (Basset et al. 2015; De Aquino et al. 2022). Among insects, ants represent a highly diverse group (Andrade-Silva et al. 2022), whose species interact with plants in different ways, playing important structuring roles (Del-Claro and Torezan-Silingardi 2009; Del-Claro et al. 2018; Moura and Del-Claro 2023). Ants, for example, play a role in seed dispersal (Fontenele and Schmidt 2021), plant defence against herbivory (Pereira et al. 2020) and pollination (Delnevo et al. 2020). Among these, ant–plant interactions mediated by extrafloral nectaries exemplify a classic plant defence strategy. In these interactions, ants feed on nectar produced by glands known as extrafloral nectaries, while protecting their host plants from herbivorous insects (Calixto et al. 2021). In general, these are facultative associations, characterised by low fidelity between the interacting partners (Dáttilo, Marquitti, et al. 2014). However, they can reduce herbivory on host plants (Pereira et al. 2020) and positively affect the survival, growth and reproduction of ants (Calixto et al. 2021).

In tropical ecosystems, extrafloral nectaries constitute an abundant and widespread food resource, exploited by a large number of ant species (Dáttilo, Marquitti, et al. 2014; Nogueira et al. 2020; Miranda et al. 2025) and produced by many plant species (Aguirre et al. 2013; Marazzi et al. 2013; Miranda et al. 2024). This association is particularly prominent in Leguminosae, a plant family rich in species bearing extrafloral nectaries (Marazzi et al. 2019). Despite the high number of ant species often sharing the same nectar sources, coexistence may be facilitated by stabilising mechanisms in interspecific competition. In this context, the facultative nature of ant–plant interactions (Dáttilo, Marquitti, et al. 2014), together with the wide availability of alternative food resources in tropical environments, likely plays a key role. An additional mechanism that may contribute to coexistence is temporal niche partitioning (Chesson 2000; Chase and Leibold 2003). For instance, in tropical savannas, ants and spiders that feed on extrafloral nectaries are able to coexist through temporal niche specialisation, in which ants feed on these glands mainly during the rainy months and spiders during the dry months (Lange et al. 2000). Moreover, pronounced shifts in the identity of highly interactive ant species associated with extrafloral nectaries between day and night have been documented in more arid environments (Dáttilo, Fagundes, et al. 2014; Schramm et al. 2023).

In highly seasonal environments, daily fluctuations in the volume and concentration of extrafloral nectar have been documented for several plant species (Anjos et al. 2016; Lange et al. 2017). Under stronger daytime water stress, nectar tends to be more concentrated in sugars, potentially altering the attractiveness of these resources to different consumers throughout the day (Chavarro-Rodríguez et al. 2013). Despite this evidence from seasonal systems, no studies have yet investigated daily variation in ant–plant interactions mediated by extrafloral nectaries in tropical forests. Nevertheless, a turnover of ant species exploiting these glands over the daily cycle is likely to occur, as many tropical ant species exhibit marked diel variation in foraging activity (General et al. 2020), with some being strongly associated with nocturnal periods (Houadria et al. 2015; General et al. 2020). In this context, investigating the dynamics of ant–plant interactions on a daily timescale in tropical forests represents a valuable opportunity to improve our understanding of the mechanisms underlying the exceptionally high diversity of these systems. Moreover, such information can inform the definition of appropriate sampling periods in studies of ant–plant interactions across different environmental contexts, helping to ensure that both interacting communities are adequately represented.

To assess the daily dynamics of these ant–plant interactions at the community level, two analytical approaches can be recommended: complex ecological networks (Bascompte et al. 2003; Bascompte and Jordano 2007) and beta diversity of interactions (Poisot et al. 2012; Ratoni et al. 2025). Complex networks have been widely used in studies on ants and plants bearing extrafloral nectaries (EFN-bearing plants) in different temporal and spatial gradients (Luna et al. 2018; Dáttilo and Vasconcelos 2019; Juárez-Juárez et al. 2023; Miranda et al. 2025). These ecological networks are mathematical representations of interactions, in which different ant and plant species are depicted as nodes and their interactions as links (Dáttilo, Marquitti, et al. 2014). This approach allows the acquisition of relevant information about the structural organisation of the interacting communities (Vázquez et al. 2009). In general, these associations mediated by extrafloral nectaries exhibit a low degree of specialisation and a nested pattern, in which species with few links tend to associate with highly interactive species and rarely with poorly interactive partner species (Dáttilo, Marquitti, et al. 2014; Miranda et al. 2022). The interesting aspect of the second approach, the beta diversity of interactions, is that it allows capturing the turnover of interacting species along temporal and spatial gradients, as well as the rewiring of the interactions along such gradients (Poisot et al. 2012). Luna et al. (2018), in a study on ant–plant interactions conducted in two desert environments, recorded a substantial turnover of species and interaction rewiring between day and night periods.

In this study, we aimed to understand the temporal dynamics of ant–plant interactions in tropical forests on a daily timescale, through structural changes in complex networks and variations in interaction beta diversity. Based on daily variation in extrafloral nectar production in more arid environments (Lange et al. 2017) and in the foraging activity of different ant species in tropical forests (General et al. 2020), we expect to find differences in the number of interactions, network size, diversity of interactions, network specialisation and nestedness among the three periods of the day. We also combined data from two consecutive periods to simulate commonly adopted sampling practices in ecological field studies, which typically focus on diurnal activity or consecutive shifts. We expect that networks with accumulated data from three periods will show substantial increases in some network descriptors compared to networks with accumulated data from two or a single period, thereby evidencing a temporal turnover of interactions throughout the day. We also postulate that the central core of highly interactive ant species in the network changes throughout the day, mainly due to nocturnal ant activity. Consequently, we expect the beta diversity of interactions to be higher between the afternoon and night, and between the night and morning, than between the morning and afternoon.

2 | Methods

2.1 | Study Area

Fieldwork was carried out in a forest fragment within the Catuaba Experimental Farm (10°04′ S, 67°37′ W), located in the municipality of Senador Guiomard, state of Acre, in the southwestern Brazilian Amazon. This forest fragment has an area of 1166 ha and the vegetation type is open rainforest with palm trees and dense rainforest with bamboo (Silveira et al. 2020). The canopy height ranges from 20 to 40 m, with emergent trees reaching up to 45 m (Silveira et al. 2020). This region has a monsoon climate (Am), with an average annual precipitation of 1900–2200 mm, and two seasons (Alvares et al. 2014). The dry season, with reduced average monthly precipitation, occurs from June to August, and the rainy season from September to May (Alvares et al. 2014). The average annual temperature is 24.5°C, with a daily variation of ±7.5°C (Silveira et al. 2020).

2.2 | Ant-Plant Interaction Collection and Processing

We sampled ant–plant interactions mediated by extrafloral nectaries in nine 150 × 10 m (1500 m^2) plots. These plots were established every 500 m along a 5 km east–west trail, following the RAPELD sampling design (Magnusson et al. 2013). In the morning (between 7 AM and 11 AM), we slowly walked through a sampling plot, searching for EFN-bearing plants at heights accessible to the collector (ranging from 0.5 to 3 m) that were interacting with ants (Dáttilo and Dyer 2014). Interactions were confirmed when ants kept their mouthparts in contact with the extrafloral nectaries of a plant for several minutes (Dáttilo, Marquitti, et al. 2014). We also searched for plants with apparently active extrafloral nectaries on young branches, but that were not interacting with ants in the morning. All these selected EFN-bearing plants were marked and sequentially coded. For interacting plants, ants were collected with entomological tweezers, and to record individuals that dropped from the plant at the slightest sign of disturbance, an entomological umbrella was positioned under the branches before collection (Dáttilo, Marquitti, et al. 2014). We assigned the same plant code to each ant, enabling tracking of this interaction. Observations on each marked plant (with or without ant association) lasted an average of 3 min. We took care to maintain a distance of at least 10 m between EFN-bearing plants sampled, to minimise the possibility of collecting individuals from the same ant colony foraging on different plants (Dáttilo and Dyer 2014). All plants marked in the morning were revisited once in the afternoon (between 1 PM and 5 PM) and once at night (between 7 PM and 11 PM). Therefore, the same number of EFN-bearing plants was observed in the three periods. Whenever we detected ants feeding on the extrafloral nectaries of a marked plant, we followed the same procedure to collect vouchers of the interacting ants. To facilitate locating the marked plants at night, in the morning, we tied a fluorescent-coloured tape to a plant near each marked plant. At night, these fluorescent-coloured tapes were easily found with long-range flashlights and headlamps. Finally, after the night samplings, we collected one sample from each marked plant for further identification.

Considering the phenological variation of EFN-bearing plants (Falcão et al. 2016; Nogueira et al. 2020; Miranda et al. 2025), we performed two samplings per plot, each including observations in the morning, afternoon and night. The first sampling occurred during the rainy season, from January to March 2024, and the second during the dry season, from June to August 2024. All observations were conducted by the same three trained observers, experienced in detecting interactions between ants and EFN-bearing plants in tropical forests, across all plots. During the dry season, samplings of each plot were carried out in the morning, afternoon and night on the same day (one plot per day). During the rainy season, when it rained between sampling periods, the observations were cancelled but resumed the following day immediately as an attempt to control for more pronounced climatic variations.

We identified the ants to species or morphospecies using identification keys (Mackay and Mackay 2010; Ortiz and Fernández 2011; Baccaro et al. 2015; Feitosa and Prada-Achiardi 2019; Mackay and Mackay 2019; Pedraza and Fernández 2019; Ward 2019; Camacho et al. 2020; Oliveira et al. 2021; Feitosa and Dias 2024; França et al. 2024) and by comparison with voucher photos in Antweb (AntWeb 2026) and specimens deposited at the Community Ecology Lab of the Universidade Federal do Amazonas, where the voucher specimens were deposited.

We identified EFN-bearing plants to the genus level using standard identification guides (Ribeiro et al. 1999; Pennington et al. 2004), complemented by comparisons with voucher specimens deposited in the herbarium of the ParqueZoobotanico of the Universidade Federal do Acre. These vouchers originate from a previous study on the morphology of extrafloral nectaries conducted in the same forest fragment and nearby areas (Miranda et al. 2024) and were used as reference material to define species and morphospecies in the present study. Species delimitation was based on leaf and stem characteristics, as well as on the morphology and position of extrafloral nectaries on the plant body (Table S2). Identification to the species level was possible for only a few taxa due to the limited availability of flowering material. The accession numbers of the reference EFN-bearing plant specimens are provided in Table S2. The voucher specimens from our work are deposited in the Laboratório de Botânica e Ecologia Vegetal of the Universidade Federal do Acre.

2.3 | Data Analysis

We used an interaction network approach to investigate potential daily changes in the structural organisation of ant–plant interactions mediated by extrafloral nectaries. For this purpose, we organised the sampled data into quantitative matrices, in which the elements (a_{ij}) represented the frequency (i.e., the number of times) with which plant species i interacted with ant species j within the plot (Bascompte et al. 2003). For each of the nine plots, we built a matrix of ant–plant interaction data sampled in the morning (M networks), another with data sampled in the afternoon (A networks), and a third with data sampled at night (N networks), for a total of 27 matrices, each representing a single-period network. To organise these matrices, we combined data from samplings conducted during both the rainy and dry seasons. We also built matrices for each plot, containing accumulated data from two consecutive periods of the day (two-period networks): morning and afternoon (M + A networks), afternoon and night (A + N networks), and night and morning (N + M networks). In these matrices, we also combined data collected during both the rainy and dry seasons, treating the presence of the same ant species on a plant across two consecutive periods as a single interaction, yielding an additional 27 matrices. This combination of consecutive periods aimed to simulate typical field sampling protocols that often focus on diurnal activity (morning + afternoon) or consecutive shifts, thereby providing a more realistic basis for comparison. Finally, for each plot, we also constructed a matrix that accumulated data from all three periods of the day (M + A + N networks) and from both rainy and dry seasons, resulting in nine matrices with comprehensive data. In these matrices, we also considered the presence of the same ant species on a plant during three periods as a single interaction.

In total, we built 63 quantitative matrices (i.e., 63 ant–plant networks), and for each of them, we calculated five network descriptors to characterise ant–plant interactions at different time intervals: number of interactions, network size, diversity of interactions, network specialisation and nestedness (using both quantitative and binary data). The number of interactions represents the total number of interactions observed in the network, including all ant and plant species in a given matrix (Dáttilo, Fagundes, et al. 2014). To calculate the network size, we multiplied the number of EFN-bearing plant species by the number of ant species in each matrix. We calculate the diversity of interactions using the H' index, which is based on Shannon's diversity index and ranges from zero to infinity (Bersier et al. 2002). We estimated specialisation using the H_2' index, which describes how species restrict their interactions relative to those expected by chance given a partner's availability (Blüthgen et al. 2006). In this index, values close to zero indicate a low level of specialisation in an ecological network, whereas $H_2' = 1$ represents complete specialisation.

We used the NODF-metric (Nestedness Based on Overlap and Decreasing Fill) (Almeida-Neto et al. 2008) to estimate the degree of nestedness in our networks with binary data, and the WNODF-metric (Weighted Nestedness Metric Based on Overlap and Decreasing Fill) (Almeida-Neto and Ulrich 2011) to estimate quantitative nestedness. In binary nestedness, all interactions are considered ecologically equivalent, and differences among them are ignored (Almeida-Neto and Ulrich 2011). Conversely, in quantitative nestedness, the weight of interactions is based on the abundances of the interacting partners (Almeida-Neto and Ulrich 2011). The values of both nestedness indices ranged from 0 (non-nested) to 100 (perfectly nested). We calculated the NODF-metric with the ANINHADO software (Guimarães and Guimarães 2006), and we estimated the NODF significance using p values based on Null Model II (1000 randomisations), for which the probability of an interaction occurring is proportional to the observed number of interactions of both plant and ant species (Bascompte et al. 2003). We estimated WNODF significance using p values based on a null model (1000 randomisations), generated using the r2dtable algorithm (Patefield 1981), which holds the marginal totals constant (i.e., observed row and column totals) whilst allowing connectance to vary. We calculated diversity of interactions, network specialisation and WNODF using the 'bipartite' package (Dormann et al. 2025) in R software, version 4.4.1 (R Core Team 2024).

We used generalised linear mixed models (GLMMs) (Bolker et al. 2009) and linear mixed-effects models (LMMs) (Crawley 2012) to test whether the ant–plant network descriptors differed among the three periods of the day. We considered each network descriptor (network size, number of interactions, diversity of interactions, network specialisation and nestedness) calculated from the single-period networks (M, A and N networks) as a response variable, and the three periods of the day (M, A and N) as an explanatory variable. We also included the identity of each plot as random effects in the models to account for repeated measures within plots and to control for temporal pseudoreplication. We tested the models' significance via analysis of variance between the evaluated model and the null model (intercept and random effect only). Subsequently, we performed contrast tests to verify pairwise differences among the three periods of the day. We also performed residual analysis and tests for overdispersion (Crawley 2012) to verify the adequacy of the models' predictions. We examined the network size and number of interactions through a GLMM with Poisson error distribution, and the diversity of interactions, network specialisation and nestedness (NODF and WNODF) through a LMM with Gaussian error distribution.

We employed a similar analytical scheme to investigate whether network descriptors varied across longer time intervals. For these models, we considered each network descriptor calculated from the two-period networks as a response variable and the different time intervals (M + A, A + N and N + M) as explanatory variables. Finally, we calculated the increase or decrease in network descriptor values from the three-period networks (M + A + N) relative to those calculated from the single-period and two-period networks. We chose not to include the different time intervals (M, A, N, M + A, A + N, N + M and M + A + N) in the same model, as their respective matrices were based on different sampling efforts.

We also evaluated the constancy of the central core of highly interacting species among different periods of the day (M, A and N). For this, we categorised ant and plant species according to Dáttilo et al. (2013): $G_c = (k_i - k_{\text{mean}})/\sigma_k$, where k_i = mean number of links for a given plant/ant species, k_{mean} = mean number of links for all plant/ant species in the network, and σ_k = standard deviation of the number of links for plant/ant species. Species with $G_c \geq 1$ belong to the generalist core of highly interacting species within the network, as they exhibit a higher number of interactions compared to other species at the same trophic level. In contrast, species with $G_c < 1$ are located at the periphery of the network, as they exhibit a lower number of interactions compared to other species at the same trophic level.

To assess total beta diversity of interactions (β_{WN}) across different periods of the day, we applied the framework proposed by Poisot et al. (2012). This index is derived from Whittaker's (1960) beta diversity index (β_W), which considers the number of shared species and the number of unique species between two communities, and ranges from zero to one, where zero indicates that the two communities have completely similar species and one indicates that they have completely different species. The total beta diversity of interactions (β_{WN}), in turn, expresses the dissimilarity of interactions and can be partitioned into two additive components: species turnover (β_{ST}) and interaction rewiring (β_{OS}). The species turnover (β_{ST}) reflects changes in the identity of interactions due to spatial or temporal changes in species composition and interaction rewiring (β_{OS}) reflects changes in the identity of interactions generated by the reassembly of interactions between the same species in different sites or sampling periods (Luna et al. 2018; Dáttilo and Vasconcelos 2019). The contribution of each component (β_{ST} and β_{OS}) to the dissimilarity of interactions can be expressed by stating its relative impact on the composition of total beta diversity of interactions (β_{WN}), through standardising the calculated values: β_{ST}/β_{WN} and β_{OS}/β_{WN} (Luna et al. 2018). Therefore, higher values of β_{ST} indicate greater interaction turnover generated by the loss or gain of species, while higher values of β_{OS} indicate greater changes in who is interacting with whom (i.e., interactions are reassembled).

For each plot, we calculated the values of β_{WN}, β_{ST} and β_{OS} between morning and afternoon, afternoon and night, and night and morning. We used linear mixed-effects models (LMMs) (Crawley 2012) to test whether these indices varied across the different periods of the day. We considered total beta diversity of interactions (β_{WN}), species turnover (β_{ST}) and interaction rewiring (β_{OS}) as response variables, and the different pairwise combinations of periods of the day (M and A, A and N, and N and M) as the explanatory variables. We also included the identity of each plot as random effects in the models to account for variance associated with random site effects. Subsequently, we performed contrast tests to verify pairwise differences between the β_{WN}, β_{ST} and β_{OS} values calculated from different pairwise combinations of periods of the day. We also performed residual analysis and tests for overdispersion (Crawley 2012) to verify the adequacy of the models' predictions.

We created GLMMs and LMMs using the 'lme4' package (Bates et al. 2025), conducted analysis of variance between each model and the null model with the 'vegan' package (Oksanen et al. 2025), ran contrast tests using the 'emmeans' package (Lenth et al. 2025) and assessed residuals of the GLMMs and LMMs with the 'DHARMa' package (Florian et al. 2025) in R version 4.4.1 (R Core Team 2024).

3 | Results

In total, we recorded 86 ant species across 22 genera and 6 subfamilies (Table S1). Of these, 30 morphospecies could not be identified to the species level and were assigned to a unique morphospecies code. We recorded 87 EFN-bearing plant species, distributed in 25 genera and 18 families (Table S2). Of these, 76 morphospecies could not be identified to the species level (67 to the genus level, seven to the family level and two with their families undetermined). As with ant species, we assigned a unique code to each plant morphospecies.

We recorded 65 ant species and 80 EFN-bearing plant species in the morning, 66 ant species and 81 EFN-bearing plant species in the afternoon, and 55 ant species and 70 EFN-bearing plant species at night (Tables S1 and S2). Six ant species (*Dolichoderus rugosus* Smith, 1858, *Dolichoderus septemspinosus* Emery, 1894, *Pseudomyrmex gracilis* Fabricius, 1804, *Pseudomyrmex* sp.3, *Pseudomyrmex* sp.9 and *Pseudomyrmex* sp.12) and two EFN-bearing plant morphospecies (*Gurania* sp.1 and *Bauhinia* sp.3) were observed interacting exclusively in the morning (Tables S1 and S2). Nine ant species (*Linepithema* sp.1, *Camponotus crassus* Mayr, 1862, *Camponotus* sp.16, *Cephalotes clypeatus* Fabricius, 1804, *Crematogaster curvispinosa* Mayr, 1862, *Cyphomyrmex* sp.1, *Solenopsis* sp.3, *Pseudomyrmex* sp.5 and *Pseudomyrmex* sp.10) and four EFN-bearing plant morphospecies (Anonacea sp.1, *Fridericia* sp.17, *Inga* sp.15 and *Solanum* sp.1) were observed interacting exclusively in the afternoon (Tables S1 and S2). Finally, nine ant species (*Dolichoderus imitator* Emery, 1894, *Camponotus atriceps* Smith, 1858, *Camponotus balzani* Emery, 1894, *Camponotus Tanaemyrmex testaceus* Emery, 1894, *Camponotus* sp.12, *Camponotus* sp.18, *Cephalotes pallidus* De Andrade, 1999, *Cephalotes* aff. *foliaceus* Emery, 1906 and *Wasmannia* sp.1) were observed interacting exclusively at night. However, no EFN-bearing plant species were observed interacting only at this period (Tables S1 and S2).

We detected significant differences in the number of interactions among ant–plant networks sampled at different periods of the day ($p < 0.001$). The N networks exhibited a lower number

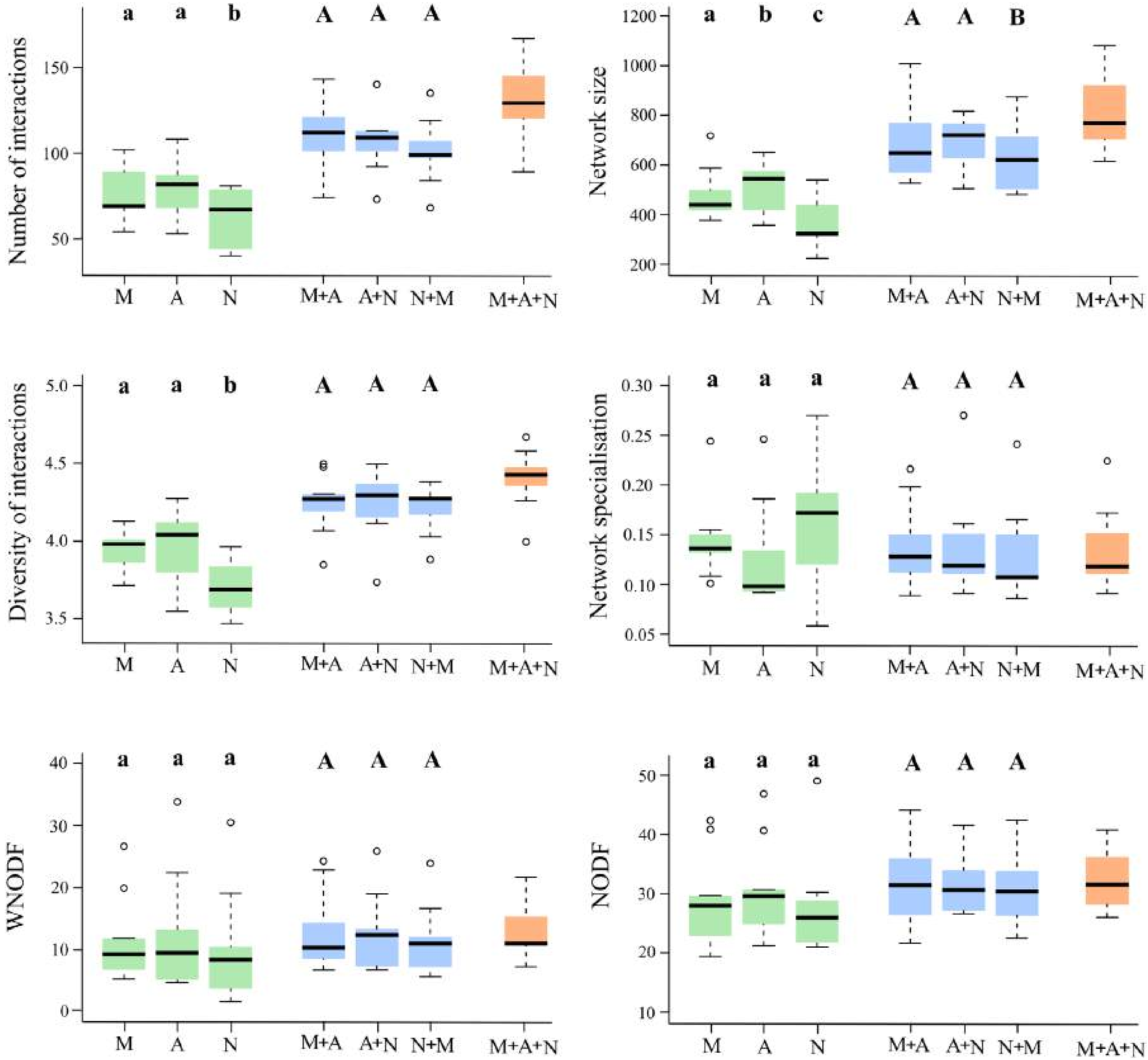

FIGURE 1 | Boxplot of ant–plant network descriptors calculated using data from a single period of the day: Morning (M), Afternoon (A) and Night (N), two periods of the day (M + A, A + N and N + M), and all three periods of the day (M + A + N), in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. The lines represent the minimum and maximum values, the box represents the first and third quartiles, and the line within the box represents the median. The letters in the graphs correspond to the results of the pairwise comparisons. Identical letters within the same analysis indicate no significant difference for the respective network descriptor among the periods or time intervals. In contrast, different letters indicate statistically significant differences in pairwise comparisons. Lowercase and uppercase letters represent outcomes from different statistical tests.

of interactions (mean ± SD) (61.11 ± 17.48) compared to M networks (76.22 ± 15.68) and A networks (74.78 ± 30.65), which did not differ from each other (Figure 1, Tables S3 and S4). Network size also varied significantly among the different periods of the day ($p < 0.001$). The N networks had smaller sizes (mean ± SD) (364.00 ± 111.68) than both M networks (478.56 ± 110.66) and A networks (516.22 ± 109.01), which also differed from each other (Figure 1, Tables S3 and S4). We further detected differences in diversity of interactions among ant–plant networks sampled at different times of day ($p < 0.001$). The N networks showed lower diversity of interactions (Mean ± SD) (3.71 ± 0.17) than the M networks (3.93 ± 0.13) and A networks (3.95 ± 0.26), which were not significantly different from each other (Figure 1, Tables S3 and S4). We did not detect significant differences in network specialisation among the different periods of the day ($p = 0.271$). None of the M networks and only 11% of the A and N networks showed significant weighted nestedness (Table S3). Additionally, we did not detect significant differences in these values among the different periods of the day ($p = 0.306$). A total of 78%, 89% and 67% of the M, A and N networks based on binary data, respectively, showed significant nestedness (Table S3). Similar to the results for weighted nestedness, we did not detect any differences in binary nestedness among the different periods of the day ($p = 0.257$).

For networks built with accumulated data from two consecutive periods, we did not detect significant differences among the different time intervals (M + A, A + N and N + M) for number of interactions ($p = 0.098$), diversity of interactions ($p = 0.305$), network specialisation ($p = 0.470$), weighted nestedness ($p = 0.128$) and binary nestedness ($p = 0.708$) (Figure 1 and Table S3). We detected significant differences only for network size ($p < 0.001$) (Figure 1 and Table S3). The N + M networks exhibited smaller sizes than M + A networks and A + N networks, which did not differ from each other (Figure 1, Tables S3 and S4). For almost all evaluated network descriptors, especially the number of interactions and network size, the three-period networks (M + A + N networks) showed increases compared to the two-period and single-period networks (Figure 1 and Table 1). For network specialisation, we did not detect any increases (Figure 1 and Table 1).

A total of 12, 11 and 13 ant species constituted the central core of the M, A and N networks, respectively. Among these, *Dolichoderus diversus* Emery, 1894 and *Crematogaster nigropilosa* Mayr, 1870 were part of the central core only in N networks (Figure 2). No ant species was exclusive to the central core of the M and A networks. A total of eight, nine and seven EFN-bearing plant species constituted the central core of the M, A and N networks, respectively. Among these, *Senegalia* sp.23 and Malpighiaceae sp.5 were part of the central core only in M networks, *Inga* sp.8 only in A networks and Malpighiaceae sp.4 only in N networks (Figure 2). We observed that in all plots, at least one ant species and one EFN-bearing plant species remained in the central core of the networks during all three periods of the day (M, A and N) (Figure 2). However, in seven plots (77.8%), we observed changes in the central core involving at least one ant species between morning and afternoon, and between afternoon and night, and in five plots (55.6%), we observed changes in the central core involving at least one ant species between night and morning (Figure 2). We observed changes in the central core involving at least one EFN-bearing plant species in eight plots (88.9%) between morning and afternoon, afternoon and night, and night and morning (Figure 2).

We found that, for all pairwise combinations of periods of the day, the interaction rewiring (β_{OS}) contributed more to the additive partitioning of the total beta diversity of interactions (β_{WN}) than species turnover (β_{ST}) (Figure 3). We detected significant differences in the total beta diversity of interactions (β_{WN}) among different pairwise combinations of periods of the day ($p < 0.001$) (Figure 4). The total beta diversity of interactions (β_{WN}) was lower between M and A networks (0.32 ± 0.07) than between A and N networks (0.46 ± 0.07) and N and M networks (0.46 ± 0.12) (Figure 4 and Table S4). However, we did not detect significant differences between the indices calculated for the A and N networks and for the N and M networks (Figure 4 and Table S4). We also detected significant differences in species turnover (β_{ST}) among different pairwise combinations of periods of the day ($p < 0.001$) (Figure 4). Species turnover (β_{ST}) was lower between M and A networks (0.11 ± 0.03) than between A and N networks (0.19 ± 0.07) and

TABLE 1 | Mean (mean ± SD) of the network descriptors calculated from matrices with data sampled at different time intervals (single period, two periods, and three periods of the day), and the increase or reduction of the descriptors calculated from matrices with data from three periods relative to those with data from a single period and two periods of the day.

Network descriptor	Mean ± SD			Average increment	
	Single period networks	Two period networks	Total networks	Total networks – single period networks	Total networks – two period networks
Number of interaction	74.93 ± 18.21	107.48 ± 20.72	130.33 ± 24.34	55.40 (42.51%)	22.85 (17.53%)
Network size	478.04 ± 132.81	705.37 ± 148.65	842.33 ± 190.28	364.29 (43.25%)	136.96 (16.26%)
Diversity of interaction	3.91 ± 0.22	4.24 ± 0.20	4.41 ± 0.22	0.50 (11.34%)	0.17 ± 0.02 (3.85%)
Network specialisation	0.14 ± 0.05	0.14 ± 0.04	0.13 ± 0.03	0.01 (8.45%)	0.01 (8.45%)
Weighted nestedness	10.95 ± 0.83	11.76 ± 6.32	12.07 ± 4.92	1.12 (9.28%)	0.31 (2.57%)
Binary nestedness	28.50 ± 8.43	30.75 ± 6.51	31.85 ± 5.27	3.54 (10.52%)	1.10 (3.45%)

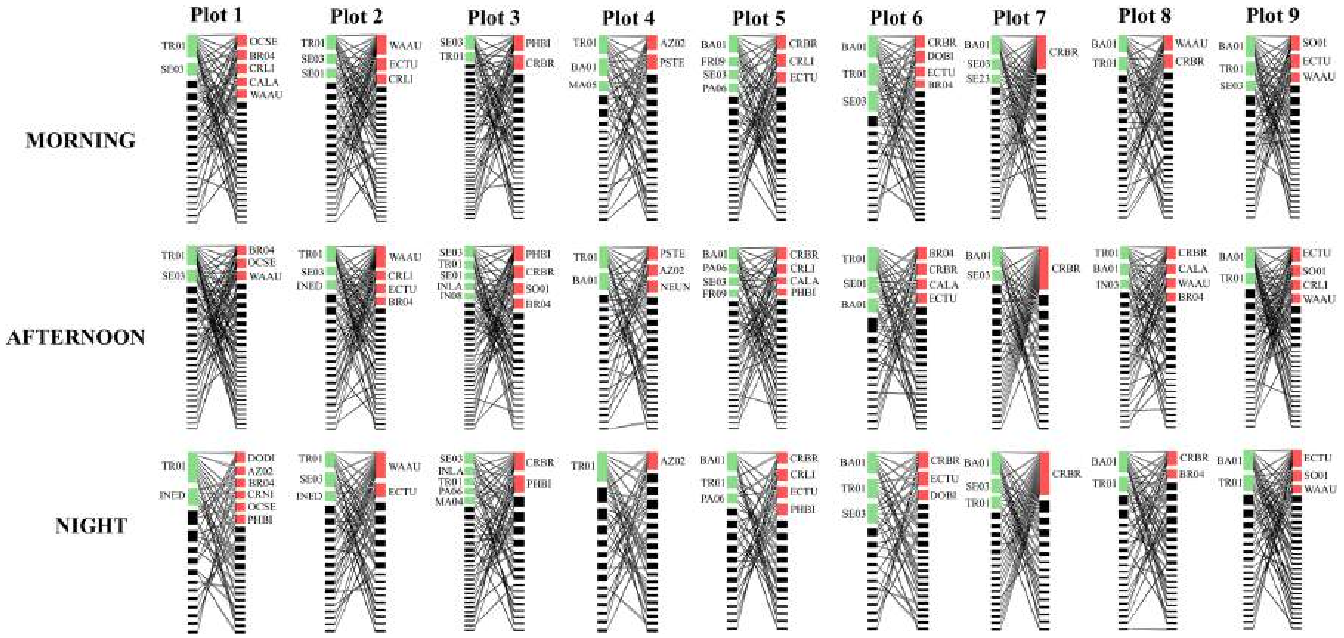

FIGURE 2 | Ant–plant networks sampled at different periods of the day (morning, afternoon and night) in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. EFN-bearing plant species belonging to the generalist core are highlighted in green, and ant species are highlighted in red. The codes for the ant and plant species are in Tables S1 and S2, respectively.

N and M networks (0.17 ± 0.05) (Figure 4 and Table S4). We did not detect significant differences in species turnover (β_{ST}) between A and N networks and N and M networks (Figure 4 and Table S4). Interaction rewiring (β_{OS}) also differs among pairwise combinations of periods of the day ($p = 0.028$) (Figure 4). β_{OS} was higher between N and M networks (0.29 ± 0.11) than between M and A networks (0.21 ± 0.05) (Figure 4 and Table S4). We did not detect differences in β_{OS} between M and A networks and A and N networks (0.27 ± 0.08), nor between N and M networks and A and N networks (Figure 4 and Table S4).

4 | Discussion

Structurally, the interactions between ants and EFN-bearing plants varied significantly throughout the day in terms of network size, number of interactions and diversity of interactions, with higher values observed in the morning and afternoon. However, network specialisation and nestedness remained stable. The beta diversity of interactions also varied throughout the day, especially during the nocturnal period. These results suggest that the apparent structural stability contrasts with marked compositional changes in species and interactions throughout the day. Thus, while global network properties such as specialisation and nestedness remain invariant, the identity of interacting species and the configuration of their links are dynamic, revealing that stable network architecture can coexist with substantial temporal turnover in interaction composition.

Although the same number of EFN-bearing plants in each sample plot was observed in all three periods, the diurnal networks showed larger network sizes and greater diversity of interactions than the nocturnal networks, due to the greater richness of plants and especially of ants observed interacting during the day (Table S5). Of the 87 EFN-bearing plant species and 86 ant species recorded in this study, 17 and 30, respectively, were not observed interacting at night (Tables S1 and S2). Ants are ectothermic organisms whose behaviour, distribution and physiology are regulated by temperature (Roeder et al. 2021). In the tropics, although species generally have high thermal tolerance (Kaspari et al. 2015; Kaspari et al. 2016), they exhibit a narrower tolerance range and tend to be thermal specialists (Janzen 1967; Stevens 1989; Gaston et al. 2009). Thus, the greater ant richness feeding on extrafloral nectar during the day may be related to the adequate and relatively constant temperatures throughout the morning and afternoon, provided by the dense vegetation cover (Kaspari and Weiser 2000; Houadria et al. 2015; General et al. 2020; Schornobay-Bochenski et al. 2025). The lower ant richness in these glands at night may reflect the internal circadian rhythms of several diurnal species (Sudd 1967), as well as ecophysiological constraints on nocturnal species, which, even in tropical environments, may exhibit lower thermal tolerance (Garcia-Robledo et al. 2017). We cannot disregard possible variations in volume and concentration of extrafloral nectar secreted by different plant species throughout the day (Anjos et al. 2016; Lange et al. 2017). In highly seasonal environments, some plant species may secrete extrafloral nectar with a higher sugar concentration during the day (Anjos et al. 2016; Lange et al. 2017), whereas others may secrete larger volumes at night (Lange et al. 2017). In our study, variations in nectar volume and concentration throughout the day may also result in greater ant attraction to these plants during diurnal periods. This is because we observed not only more ant species in the extrafloral nectaries in the morning and afternoon, but also a greater number of interactions. Regarding the plants, we acknowledge limitations in morphospecies determination, since identifications were mainly based on vegetative structures. However, since we assigned the same morphospecies to each plant individual in the morning, afternoon and night, we believe that any errors

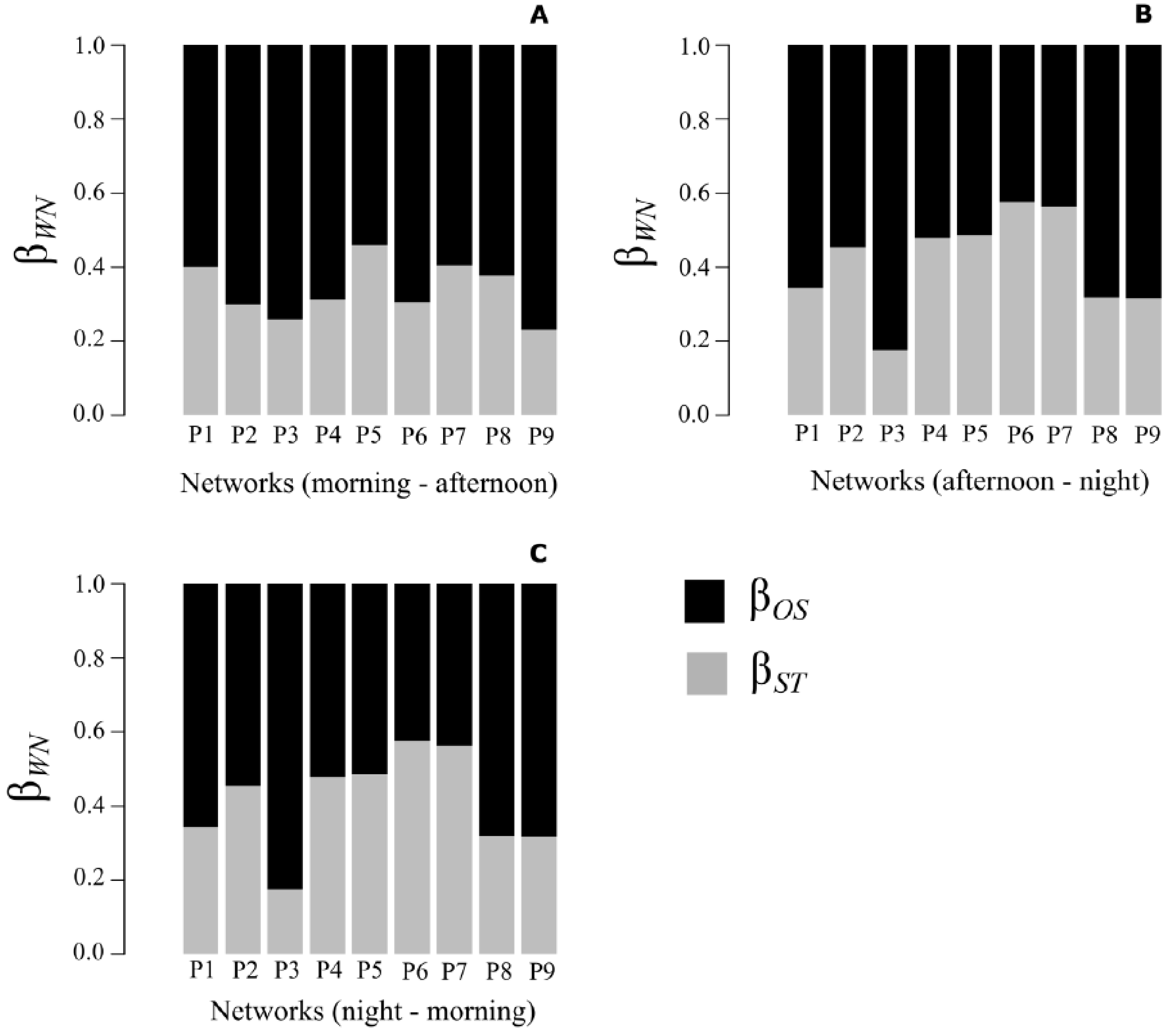

FIGURE 3 | Proportion of additive partition of total beta diversity of interactions (β_{WN}) recorded in three periods of the day (morning, afternoon and night), in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. Each bar represents the standardised value of interaction turnover. In black, the species turnover generated by changes in species composition (β_{ST}); in grey, the interaction rewiring (β_{OS}). The values of the additive partition were determined by dividing each calculated value of β_{ST} and β_{OS} by β_{WN}. Graph 'A' is relative to the beta diversity of interactions between morning and afternoon, 'B' between afternoon and night and 'C' between night and morning.

occurring at similar rates across the three periods should not affect the detection of daily variations in network size and diversity of interactions.

Although the number of interacting species recorded in nocturnal networks was lower, network specialisation and nestedness remained stable throughout the three periods. Similar nestedness stability throughout the day for these ant–plant interactions has been recorded in other environments, such as the Brazilian Cerrado and the desert (Dáttilo, Fagundes, et al. 2014; Luna et al. 2018; Schramm et al. 2023). In these interactions, some generalist ant and plant species, generally widely distributed on a small scale (Dáttilo et al. 2019), provide substantial stability to the nested structure of these networks (Díaz-Castelazo et al. 2010), even after disturbances caused, for example, by tropical hurricanes (Sánchez-Galván et al. 2012) and forest fragmentation (Miranda et al. 2022). These networks also include less frequent species, which vary much more along spatial gradients but contribute very little to the overall structure of these networks (Dáttilo et al. 2013; Dáttilo et al. 2019). In our study, the ant species *Crematogaster brasiliensis* Mayr, 1878, *Wasmannia auropunctata* Roger, 1863 and *Ectatomma tuberculatum* Olivier, 1792, and the plant species *Bauhinia* sp.1, *Triplaris* sp.1 and *Senegalia* sp.3 were the most dominant in all sampled plots and in all three periods. In addition to these, other ant species such as *Azteca* sp.2, *Brachymyrmex* sp.4, *Camponotus latangulus* Roger, 1863, *Ochetomyrmex semipolitus* Mayr, 1878, *Pheidole biconstricta* Mayr, 1870 and *Solenopsis* sp.1 were also frequently recorded in all three periods. Except for *E. tuberculatum*, all other ant species mentioned showed numerical competitive

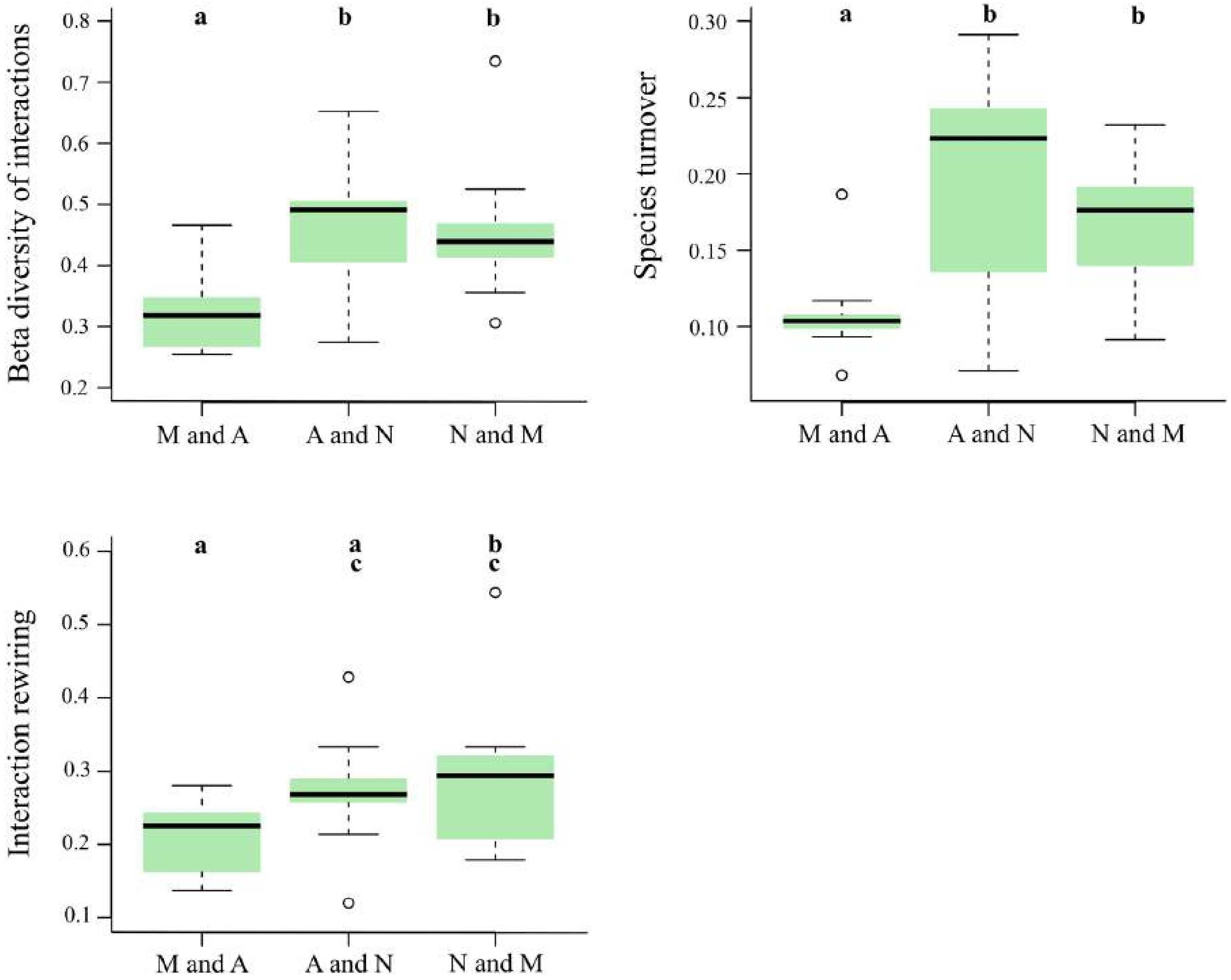

FIGURE 4 | Boxplot of beta diversity of interactions (β_{WN}), species turnover (β_{ST}) and interaction rewiring (β_{OS}) between different pairs periods of the day (M and A, A and N, and N and M), in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. The lines represent the minimum and maximum values, the box represents the first and third quartiles, and the line within the box represents the median. The letters in the graphs correspond to the results of the pairwise comparisons. Identical letters in the same graph indicate no significant difference for the respective index among the periods. In contrast, different letters indicate statistically significant differences in pairwise comparisons.

dominance (Rico-Gray and Oliveira 2007). For them, it was common to find a dozen or more individuals on the same branch with active glands (personal observations). This is a common competitive strategy among ant species that feed on extrafloral nectaries (Rico-Gray and Oliveira 2007; Dáttilo, Marquitti, et al. 2014) and, in the present study, appears to play an important role in the daily stability of the nested structure of these networks.

We detected substantial increases in network size and the number of interactions in networks with accumulated data across three periods, compared to networks with two or a single period, revealing turnover of species throughout the day. Thus, ecological conclusions based on diurnal field activities or on consecutive periods should be drawn with caution. Of the 86 ant species recorded, 24 (28%) were recorded exclusively in a single period and 20 (23%) in only two periods, most of them being species with low frequency in the networks. Changes between highly interactive ant species throughout the day were also detected. Approximately 70% of the networks showed daily changes in the composition of their central cores involving at least one highly interactive ant species. *Dolichoderus diversus* and *Crematogaster nigropilosa*, for example, were species belonging exclusively to the nocturnal network cores. However, across all networks, at least one highly interactive ant species remained in the central core throughout all three periods. In the Brazilian Cerrado, more pronounced changes in highly interactive ant species in the central cores between day and night have been detected, possibly due to the greater daily temperature range of these ecosystems (Dáttilo, Fagundes, et al. 2014). Regarding the EFN-bearing plants, only six (7%) of the 87 species recorded were exclusive to a single period. All networks showed one to two highly interactive plant species that remained in their central cores across the three periods, yet they also exhibited daily changes in composition involving at least one species. For EFN-bearing plants, however, interpretations of compositional change should be made cautiously, given that uncertainties in morphospecies delimitation may partly influence the detected patterns.

These changes in interacting species throughout the day were also captured by the analyses of beta diversity of interactions. Higher values of total beta diversity of interactions (β_{WN}) were observed between the afternoon and night networks and between the night and morning networks. We observed similar results for both additive components. Species turnover (β_{ST}) between the morning and afternoon was almost half of the species turnover (β_{ST}) recorded between the nocturnal and both diurnal periods. Nine ant species were collected exclusively at night, five of which belong to the genus *Camponotus*, known for the nocturnal behaviour of several species (Menzi 1987; Klotz and Reid 1993; Sharma et al. 2004). These species exhibit adaptations that allow them to forage at night, such as larger eyes and a greater number of ommatidia (Menzi 1987), and they respond to visual and tactile cues, including moonlight and landmarks within the tree canopy (Klotz and Reid 1993). In addition, other species such as *Dolichoderus superaculus* Lattke, 1987, *Dolichoderus diversus*, *Camponotus* (*Tanaemyrmex*) sp.1 and *Paraponera clavata* Fabricius, 1775 were much more frequent at night. *P. clavata* is a nocturnal neotropical species that nests on the ground at the base of EFN-bearing trees (Dejean et al. 2007). They feed on the extrafloral nectaries of these trees at night, remaining in their nests during the day, while other ant species can exploit this resource (Hölldobler and Wilson 1990). In contrast, species of the genus *Pseudomyrmex* were recorded mainly during the diurnal periods. Of the 11 *Pseudomyrmex* species sampled, only *Pseudomyrmex concolor* Smith 1860 was recorded in extrafloral nectaries at night. These results provide evidence of niche temporal partitioning on a daily timescale.

Temporal niche partitioning tends to stabilise interspecific competition and favour the coexistence of species that use the same resource (Chesson 2000; Chase and Leibold 2003). Among ants, this pattern on a daily timescale has been observed across different ecosystems, including pastures (Albrecht and Gotelli 2001), tropical forests (Houadria et al. 2015) and deserts (Luna et al. 2018). In the Brazilian Cerrado, it has been documented even among ant species that feed on extrafloral nectar (Dáttilo, Fagundes, et al. 2014; Lange et al. 2017), indicating strong interspecific competition over this resource. As discussed above, in our study, some numerically dominant ant species remained in the central cores of the networks throughout all three periods, exerting continuous competitive pressure on the other species. Among the peripheral ant species, more restricted to one or two periods, some genera such as *Camponotus*, *Pseudomyrmex* and *Paraponera* have aggressive species that tend to compete by the displacement of competitors (Hölldobler and Wilson 1990; Breed et al. 1991; Espírito Santo et al. 2011; Barnett et al. 2014). Therefore, the turnover of these ant species throughout the day, especially at night, may reduce interspecific competition in plants not numerically dominated by the highly interactive ant species in network cores, favouring their coexistence. Together, these patterns suggest that the nocturnal period acts as a stronger ecological filter on the network, restricting participation to a smaller set of ant species while amplifying the relative influence of competitively dominant and behaviourally specialised taxa.

In addition to the turnover of interacting species, the interaction rewiring (β_{OS}) also varied throughout the day in all plots. The additive component represented the largest contribution to total interaction beta diversity (β_{WN}), a pattern also reported for arboreal ant communities in desert environments (Luna et al. 2018). Our results indicate that these interactions change throughout the day in tropical forests, even when the same interacting species are involved. This rewiring of interactions between periods, especially with the nocturnal period, indicates that ants displace between EFN-bearing plants throughout the day, in accordance with the facultative nature of these associations (Dáttilo, Marquitti, et al. 2014). These displacements may be related, for instance, to variations in the quantity or quality of extrafloral nectar secreted throughout the day by different species (Anjos et al. 2016; Lange et al. 2017; Alencar et al. 2023). Considering the effects of leaf damage caused by herbivorous insects on the increased productivity of extrafloral nectaries (Ness 2003), daily variations in the activity of these herbivores may also favour the interaction rewiring in these networks throughout the day. Finally, we acknowledge that this additive component is the most likely to be impacted by potential errors in plant morphospecies determination. Therefore, we will be cautious in discussing the results. However, one fact about these plants is that, in all periods, most sampled species and morphospecies exhibited either elevated or flattened extrafloral nectaries. In tropical forests located in the southwestern Brazilian Amazon, elevated and flattened extrafloral nectaries are observed mainly in species of the Fabaceae and Bignoniaceae families (Miranda et al. 2024). Both extrafloral nectary morphotypes offer advantages in attracting ants. Elevated extrafloral nectaries tend to secrete high volumes of nectar due to their larger sizes (Díaz-Castelazo et al. 2005), and flattened extrafloral nectaries can be advantageous because they generally occur in greater numbers in the same location, which ensures the secretory activity of the branch even after damage to some of these glands (Elias and Gelband 1976). Thus, the high frequency of these two advantageous morphotypes of extrafloral nectaries in our samples suggests the effectiveness of the ant defence system against herbivory in this forest.

We describe some aspects of the daily dynamics of ant–plant interactions mediated by extrafloral nectaries in a tropical forest of the Brazilian Amazon. The nested pattern of these interactions remained stable throughout the day, possibly due to the persistence of some dominant ant species on different EFN-bearing plants during all three periods. The network size and diversity of interactions were greater in the morning and afternoon, indicating a higher number of species interacting during the diurnal periods. Different factors may be triggering this pattern, such as the low daily temperature range caused by dense vegetation, temperature tolerance restrictions in some nocturnal ant species, and variations in the volume and concentration of extrafloral nectar throughout the day among different plant species. We also detected an increase in network size and the number of interactions when combining data across three periods, indicating species turnover throughout the day, especially among ants. Temporal niche partitioning at the daily scale may be a key mechanism by which ant communities reduce direct competition while maintaining high levels of species coexistence in systems mediated by extrafloral nectaries. Our results indicate that daily temporal dynamics are important for the organisation and maintenance of ant–plant networks mediated by extrafloral nectaries in tropical forests, and that sampling across multiple daily periods provides a more comprehensive understanding of these interactions.

Author Contributions

Patrícia Nakayama Miranda: conceptualization, data curation, methodology, investigation, formal analysis, project administration, writing – original draft, writing – review and editing. **Maiara de Souza Bento:** data curation, investigation, writing – review and editing. **Ítalo Miranda Armes:** data curation, investigation, writing – review and editing. **Izaias Brasil da Silva:** data curation, writing – review and editing. **Ricardo Eduardo Vicente:** writing – review and editing, data curation. **Fabrício Beggiato Baccaro:** data curation, formal analysis, writing – review and editing. **Wesley Dáttilo:** formal analysis, writing – review and editing, conceptualization, methodology.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** List of ant species present in the ant–plant networks sampled in three different periods of the day in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. The codes refer to the ant species that belong to the generalist core of the networks. M = morning; A = afternoon; N = night. **Table S2:** List of EFN-bearing plant species in the ant–plant networks sampled in three different periods of the day in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. The codes refer to the EFN-bearing plant species that belong to the generalist core of the networks. M = morning; A = afternoon; N = night. **Table S3:** Network size, number of interactions, network specialisation, diversity of interaction and nestedness (WNODF and NODF) of the ant–plant networks sampled in different time intervals in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. M = morning networks, A = afternoon networks, N = night networks, M + A = networks with accumulated morning and afternoon data, A + N = networks with accumulated afternoon and night data, N + M = networks with accumulated night and morning data, M + A + N = networks with accumulated morning, afternoon and night data. **Table S4:** Network size, number of interactions, network specialisation, diversity of interaction and nestedness (WNODF and NODF) of the ant–plant networks sampled in different time intervals in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon. **Table S5:** Richness of ant species and EFN-bearing plant species interacting during each of the three periods of the day (morning, afternoon and night) in nine plots of a tropical forest fragment located in the state of Acre, Brazilian Amazon.