

# The influence of spatial sampling scales on ant–plant interaction network architecture

Wesley Dáttilo<sup>1</sup>  | Jeferson Vizentin-Bugoni<sup>2</sup>  | Vanderlei J. Debastiani<sup>3</sup> | Pedro Jordano<sup>4</sup>  | Thiago J. Izzo<sup>5</sup>

<sup>1</sup>Red de Ecoetología, Instituto de Ecología A.C., Xalapa, Mexico

<sup>2</sup>University of Illinois at Urbana-Champaign, Urbana, Illinois

<sup>3</sup>Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

<sup>4</sup>Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), Sevilla, Spain

<sup>5</sup>Departamento de Botânica e Ecologia, Universidade Federal de Mato Grosso, Cuiabá, Brazil

## Correspondence

Wesley Dáttilo

Emails: wdattilo@hotmail.com; wesley.dattilo@inecol.mx

## Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 558225/2009–8

Handling Editor: Julian Resasco

## Abstract

1. Despite great interest in metrics to quantify the structure of ecological networks, the effects of sampling and scale remain poorly understood. In fact, one of the most challenging issues in ecology is how to define suitable scales (i.e., temporal or spatial) to accurately describe and understand ecological systems.
2. Here, we sampled a series of ant–plant interaction networks in the southern Brazilian Amazon rainforest in order to determine whether the spatial sampling scale, from local to regional, affects our understanding of the structure of these networks.
3. To this end, we recorded ant–plant interactions in adjacent 25 × 30 m subplots (local sampling scale) nested within twelve 250 × 30 m plots (regional sampling scale). Moreover, we combined adjacent or random subplots and plots in order to increase the spatial sampling scales at the local and regional levels. We then calculated commonly used binary and quantitative network-level metrics for both sampling scales (i.e., number of species and interactions, nestedness, specialization and modularity), all of which encompass a wide array of structural patterns in interaction networks.
4. We observed increasing species and interactions across sampling scales, and while most network descriptors remained relatively constant at the local level, there was more variation at the regional scale. Among all metrics, specialization was most constant across different spatial sampling scales. Furthermore, we observed that adjacent assembly did not generate more variation in network descriptor values compared to random assembly. This finding indicates that the spatially aggregated distribution of species/individuals and abiotic conditions does not affect the organization of these interacting assemblages.
5. Our results have a direct impact on our empirical and theoretical understanding of the ecological dynamics of species interactions by demonstrating that small spatial sampling scales should suffice to record some patterns commonly found in ant–plant interaction networks in a highly diverse tropical rainforest.

## KEYWORDS

ecological networks, network structure, plant–animal interactions, sampling scale dependence, sampling variation

## 1 | INTRODUCTION

One of the most persistent challenges in ecology is the definition of suitable scales (i.e., temporal or spatial) at which to describe an ecological system (reviewed by Chave, 2013). Recent evidence indicates that many real-world patterns and processes are context dependent, which generates non-convergent (i.e., unique) patterns across scales (Chalcraft, Williams, Smith, & Willig, 2004; Crawley & Harral, 2001; Suding, Farrer, King, Kueppers, & Spasojevic, 2015). Therefore, scale effects create fundamental problems for ecologists who work on most ecological processes, from population to ecosystem levels (Levin, 1992; Rahbek, 2005).

Understanding how and why the structure of interaction networks vary can help us better understand the role of ecological interactions in maintaining biodiversity (reviewed by Bascompte & Jordano, 2014; Dáttilo & Rico-Gray, 2018; Vázquez, Blüthgen, Cagnolo, & Chacoff, 2009). However, the effect of spatial scale (local vs. regional) on ecological network analysis (but see Pillai, Gonzalez, & Loreau, 2011; Roslin, Várkonyi, Koponen, Vikberg, & Nieminen, 2014; Thompson & Townsend, 2005; Trøjelsgaard & Olesen, 2016; Wood, Russell, Hanson, Williams, & Dunne, 2015) is frequently not explicitly considered in the literature (Chacoff et al., 2012; Gibson, Knott, Eberlein, & Memmott, 2011; Jordano, 2016; Nielsen & Bascompte, 2007; Vizentin-Bugoni et al., 2016). Seminal studies that deal with the structure of ecological networks assumed that observed patterns and structuring processes are scale invariant (e.g., Bascompte, Jordano, Melián, & Olesen, 2003); however, multiple network descriptors are not scale invariant (Blüthgen, Fründ, Vázquez, & Menzel, 2008; Trøjelsgaard & Olesen, 2016). More recent studies revealed that some network structure descriptors are strongly affected by temporal scales (Falcão, Dáttilo, & Rico-Gray, 2016; Rasmussen, Dupont, Mosbacher, Trøjelsgaard, & Olesen, 2013) and time-structured sampling effort (Chacoff, Resasco, & Vázquez, 2018; Rivera-Hutinel, Bustamante, Marín, & Medel, 2012; Vizentin-Bugoni et al., 2016), and these features could lead to erroneous conclusions regarding the ecological and evolutionary dynamics of ecological networks.

Species and their ecological interactions can also vary across sampling scales (Belmaker et al., 2015; Gering & Crist, 2002; Thompson, 2005). For instance, when the spatial sampling scale is increased, the number of species and interactions (i.e., network size) and environmental heterogeneity (both biotic and abiotic) also increase, a phenomenon that generates a complex mosaic of interactions (Aizen, Sabatino, & Tylíanakis, 2012; Burkle & Knight, 2012; Carstensen, Sabatino, & Morellato, 2016; Trøjelsgaard, Jordano, Carstensen, & Olesen, 2015). In this case, spatially closer networks tend to present more similar abiotic conditions and, consequently, a reduced turnover of species and interactions (Dáttilo, Guimarães, & Izzo, 2013). Such networks are expected to present greater similarity in terms of interaction patterns than is the case with more distant networks. Despite the importance of considering the effect of sampling scale on studies of ecological networks, we are only beginning to understand how and why the

spatial sampling scale (i.e., the grain and extent of the sampling) can affect interaction network patterns (Carstensen, Trøjelsgaard, Ollerton, & Morellato, 2018). Indeed, most ecological network studies to date have only considered how structural patterns change spatially (e.g., Burkle & Alarcón, 2011; Trøjelsgaard et al., 2015; Vázquez et al., 2009) or explored the influence of animal movement in continuous space on the networks (e.g., Dupont et al., 2014; Morales & Vázquez, 2008). Recent studies highlighted that the spatial turnover of pairwise interactions between plants and pollinators can be highly variable, where distant communities present lower similarity in terms of interactions and species composition (Carstensen, Sabatino, Trøjelsgaard, & Morellato, 2014) that could influence network structure. Many of the potential mechanisms that underlie changes in network properties are therefore related to interaction rewiring (i.e., the reorganization of interactions among species over scales) and species turnover (CaraDonna et al., 2017), for instance, due to limited dispersal and phenology (Nekola & White, 1999). Further, other mechanisms that are not associated with natural history of the interacting species, such as sampling error, can also alter network properties (Falcão et al., 2016).

Mutualistic interactions between ants and plants with extrafloral nectaries (EFN-bearing plants) constitute a suitable study system with which to explore such questions. In this system, plants produce a nutritious liquid for ants that, in exchange, protect the host plant against herbivores (Rico-Gray & Oliveira, 2007). While knowledge regarding the structure and dynamics of ant-plant networks has increased over recent years (Chamberlain, Kilpatrick, & Holland, 2010; Del-Claro et al., 2016; Díaz-Castelazo, Sánchez-Galván, Guimarães, Raimundo, & Rico-Gray, 2013; Dáttilo, Rico-Gray, Rodrigues, & Izzo, 2013), we are only aware of two studies that directly tested how spatial sampling variation shapes the spatial structure of ant-plant networks (Dáttilo, Guimarães, et al., 2013; Sugiura, 2010). For instance, Dáttilo, Guimarães, et al. (2013), working with the same plots as in this study, examined whether spatially closer plots present more similar network structures compared to more distant plots. The study found a consistent and non-random pattern of ant-plant network organization that is independent of variations in local and landscape environmental factors. Some recent studies demonstrated a clear spatial structure in interaction networks (e.g., Carstensen et al., 2016; Maruyama, Vizentin-Bugoni, Oliveira, Oliveira, & Dalsgaard, 2014; Moreira, Boscolo, & Viana, 2015). However, it remains unknown how the patterns currently described for ant-plant networks depend on the utilized spatial sampling scale. A next step in the analysis of ant-plant networks would be to understand how variable spatial sampling scales influence the organization of these interacting assemblages.

In this study, we used a dataset we previously sampled to investigate whether the spatial sampling scale affects the structural patterns observed in ant-plant interaction networks. The resulting database is one of the largest compiled to date in terms of species richness and number of ant-plant interactions; it comprises a total of 881 interactions between 112 ant and 88 plant species (partially published in Dáttilo, Guimarães, et al., 2013). Specifically, we tested

whether increasing the sampling scale (from local to regional) affected the observed interaction patterns, including both binary and quantitative network descriptors. We hypothesized that, due to the considerable monopolization of food sources by a spatially and temporally constant core of competitive ant species (reviewed by Del-Claro et al., 2016), small spatial sampling scales would suffice to record the patterns commonly found in ant–plant networks. This phenomenon should occur because the core of strongly competitive (or dominant) ant species with the highest proportion of the interactions would already be recorded in the first plots sampled, and the other rare species collected as a result of increasing the sampling scale would add little information to the network structure. Some dominant ant species could therefore be more constrained in their choice of interaction partners (i.e., link conservatism) across local communities, as recently shown by Carstensen et al. (2018) for plant–pollinator networks. This effort produced data that included spatially fine-grained resolution of interaction patterns (local sampling scale) as well as distance replication (regional sampling scale) in the southern Brazilian Amazon rainforest. We compared both local and regional sampling scales since different processes and mechanisms could operate at these distinct levels. For instance, differences in landscape characteristics at local (e.g., quality of food source patches) and regional (e.g., amount of suitable available habitat) levels may favour some species while impairing others and could influence the spatial distribution of species interactions in an ecosystem. Such evaluation of species interaction pattern constancy at different spatial sampling scales should contribute to our understanding of the factors that shape the organization of ecological networks in highly diverse tropical rainforests.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Fieldwork was carried out in an undisturbed ombrophilous forest within the southern Brazilian Amazon, in the municipality of Cotriguaçu, in the northern portion of Mato Grosso state (9°48'S, 58°15'W, between 230 and 274 m a.s.l.). Vegetation in the 7,000-ha forest consists mainly of primary tropical rainforest, with canopy trees that reach 30–40 m in height and some emergent trees that reach up to 45 m. The topography in our study region varies 40 m between plateaus and valleys. Despite this relatively small difference, several studies conducted throughout Amazonia found elevation influences the structure and composition of the edaphic communities (Castilho et al., 2006; Magnusson et al., 2005; Phillips et al., 2003), which is in part due to long-term erosion processes and variation in the effects of flooding regimes. Indeed, a previous study performed at our sampling sites showed high variation in ant and plant species richness and composition over small spatial scales (5 km<sup>2</sup>; Dáttilo, Guimarães, et al., 2013). According to the Köppen classification, the regional climate is defined as tropical monsoon – Am (also known as a tropical wet), with distinct dry (May–October) and rainy (November–April) seasons. Mean annual temperature is

24°C, mean annual relative humidity is 85%, and mean annual rainfall ranges from 2,000 to 2,300 mm (Dáttilo & Dyer, 2014).

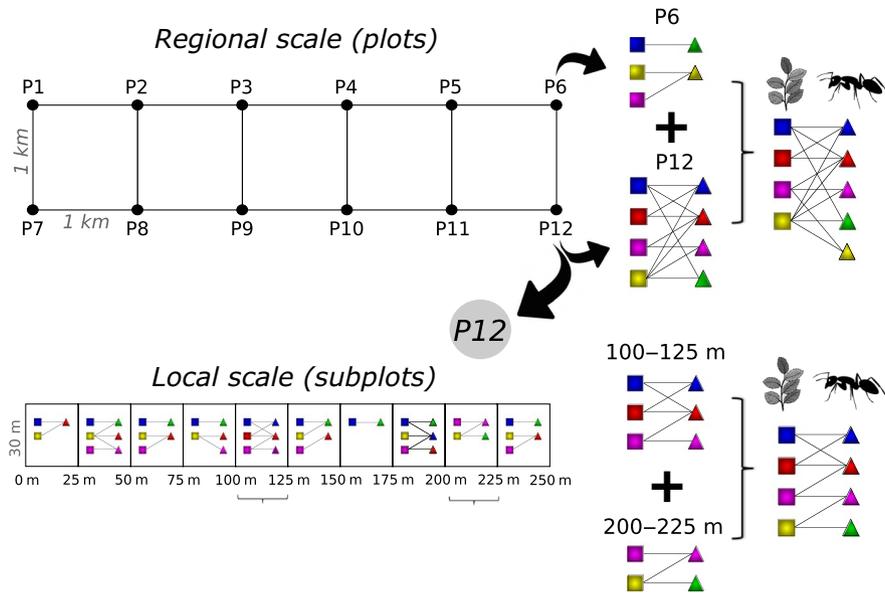
### 2.2 | Data collection

We sampled ant–plant interactions in December 2010 and January 2011 (always between 09:00 and 15:00) within a grid system managed by the Brazilian Research Program in Biodiversity (PPBio). This grid was composed of sampling plots uniformly distributed between two parallel east–west trails 5 km in length, located 1 km apart (5 km<sup>2</sup>). A sampling plot of 250 × 30 m (7,500 m<sup>2</sup>) was established every km along each trail (12 plots total). Due to the high heterogeneity in our study area (see above), we considered each of the 12 plots as an independent sample of ants and plants. In other words, we considered that the distance among sampling plots was enough to guarantee that an individual found in a plot would never interact with an individual on another sampling plot. At each plot, two researchers traversed the entire area on foot and recorded all accessible ant species that fed on EFN (from 0.5 to 3 m high). For every new observed ant–plant interaction, we recorded the exact position of the interaction on a Cartesian plane within each plot (Supporting Information Appendix S2).

### 2.3 | Spatial sampling scales

In order to investigate whether the spatial sampling scale affected the description of ant–plant networks, we used two scales. At the *local sampling scale*, we subdivided each of the 12 plots into ten 25 × 30 m (750 m<sup>2</sup>) adjacent subplots and created a continuum by combining data from these subplots (i.e., recording species richness and interactions) so that the local subplot continuum gradually increased from 750 m<sup>2</sup> (one subplot) to 7,500 m<sup>2</sup> (10 subplots) (Figure 1). One may argue that a single subplot is too small to provide an accurate description of a network; however, the single subplot has heuristic value, since the gradual accumulation of subplots can indicate at which point of the continuum a network descriptor reaches a constant value. At the *regional sampling scale*, we created another continuum by adding (i.e., increasing species richness and interactions) plots gradually up to an accumulated total of 12 plots, which increased from 7,500 m<sup>2</sup> (one plot) to 90,000 m<sup>2</sup> (12 plots) (Figure 1). Note that our spatial sampling scale is related to the ecological concept of spatial scale, which encompasses both grain (the minimum spatial resolution of the data) and extent (defined as the size of the study area). Previous studies on ant–plant networks considered only one of the two components. We conducted analyses over a large extent with a fine grain size, and this design allowed us to test whether increasing the spatial sampling scale affected the observed patterns in ant–plant networks.

We first created these local and regional continuums by adding adjacent subplots (*local sampling scale*) or nearest plots (*regional sampling scale*). However, since ants and EFN-bearing plants may be particularly aggregated in space, spatially closer plots are expected to be similar (Dáttilo, Guimarães, et al., 2013). Thus, the fixed order



**FIGURE 1** Schematic representation of sampling methods that shaped ant–plant networks at two spatial sampling scales. At the local sampling scale, we subdivided each of the 12 plots into ten  $25 \times 30$  m side-by-side subplots and a continuum was created by adding up subplots (i.e., species richness and interactions), such that the local continuum gradually increased from  $750 \text{ m}^2$  (1 subplot) to  $7,500 \text{ m}^2$  (10 subplots). At the regional sampling scale, we created a continuum by gradually adding the 12 larger plots (i.e., species richness and interactions), such that the continuum ranged from  $7,500 \text{ m}^2$  (1 plot) to  $90,000 \text{ m}^2$  (12 plots). Note that we adjacently and randomly combined subplots or plots in order to create continuums of increasing sampling spatial scales at local and regional levels, respectively (see Materials and Methods for more information)

of addition of adjacent sampling unities (subplots or plots) is prone to produce continuums that are biased towards sites particularly suitable for ant nesting. To account for these potential influences arising from juxtaposition, we used an adaptation of the rarefaction-like approach applied by Vizenin-Bugoni et al. (2016) in which we summed plots in all possible combinations regardless of their spatial position to create randomized continuums of increasing area for both local and regional sampling scales. This method is hereafter referred to as *random assembly*, while the adjacent sum of plots is called *adjacent assembly*. Note that the random (non-adjacent) aggregation of subplots or plots can be considered as a null model for a hypothesis where the clustered distribution of ants and plants would influence network metrics. In this case, if changes in network descriptors with increasing sampling scale occur faster in random compared to adjacent assembly, then the aggregation of plants and ants in space may affect the patterns of ant–plant interactions and, therefore, reveal the role of species spatial distribution as a driver of changes in network descriptors through sampling scales. The number of assembled networks for each size class of randomly assembled continuums depended on the number of possible combinations among plots in each class. Thus, at the local sampling scale, there were 120 unique subplots, which allowed for 540 combinations of two subplots, 1,440 of three subplots and 2,520, 3,024, 2,520, 1,440, 540, 120 and 12, respectively, for the subsequent increments. At the regional sampling scale, this resulted in 12 combinations of one plot, 66 of two plots and, subsequently, 220, 495, 792, 924, 792, 495, 220, 66, 12 and 1. A few combinations for local sampling led to networks that were too small to calculate some network metrics due to the low numbers of

ants and plants. We therefore removed these cases from the confidence interval calculation. Specifically, these removals represent, at most, 26.7% (32 out of 120 combinations) for a single subplot, 2.4% (13 out of 540) for two subplots and 0.1% (2 out of 1440) for three subplots. For the other combinations, it was always possible to calculate all metrics.

## 2.4 | Data analysis

Initially, we estimated the sampling completeness of our ant–plant interaction networks throughout the increasing sampling scale (similar to Chacoff et al., 2012). For this effort, we generated accumulation curves with the number of plants and ant species and distinct pairwise interactions across both local and regional sampling scales. We used the Chao2 estimator since it is one of the least biased estimators for small matrices and least sensitive to undersampling (Colwell & Coddington, 1994). To investigate the change in plant and ant composition within each subplot and among plots, we used the additive partitioning of diversity ( $\gamma = \alpha + \beta$ ) and analysed the  $\beta$ -diversity in two different spatial sampling scales:  $\beta_1$  – between subplots within each plot in a same tree and  $\beta_2$  – between plots (Veech, Summerville, Crist, & Gering, 2002).

We built a quantitative matrix of interactions (**A**) for each of the 120 subplots (local sampling scale) or 12 plots (regional sampling scale) in which elements  $A_{ij}$  represent the number of interactions between ant species  $i$  and plant species  $j$ . In order to avoid overestimation of the ant species with more efficient recruiting systems, we calculated the frequency of ant–plant interactions based on the

frequency at which an ant species was recorded interacting with a plant species in a subplot or plot, rather than the number of workers on a plant (Dáttilo, Sánchez-Galván, Lange, Del-Claro, & Rico-Gray, 2014). For each ant–plant network, we calculated the following network descriptors: plant richness, ant richness, number of ant–plant interactions (visits), binary nestedness (*NODF*), weighted nestedness (*wNODF*), specialization ( $H_2'$ ), binary modularity (*Q*) and weighted modularity (*wQ*). These measures are the most commonly used network descriptors in the literature that address ant–plant networks since they cover a wide range of possible structures with complementary biological significance, such as the overlap and distribution of interactions between species and the level of species interdependence in a community (Dormann, Fründ, Blüthgen, & Gruber, 2009). Previous studies showed that ant–plant networks mediated by EFN exhibit a binary (but not weighted) nested pattern of interactions, a non-modular pattern (considering both binary and weighted data) and an average level of network specialization (Del-Claro et al., 2018).

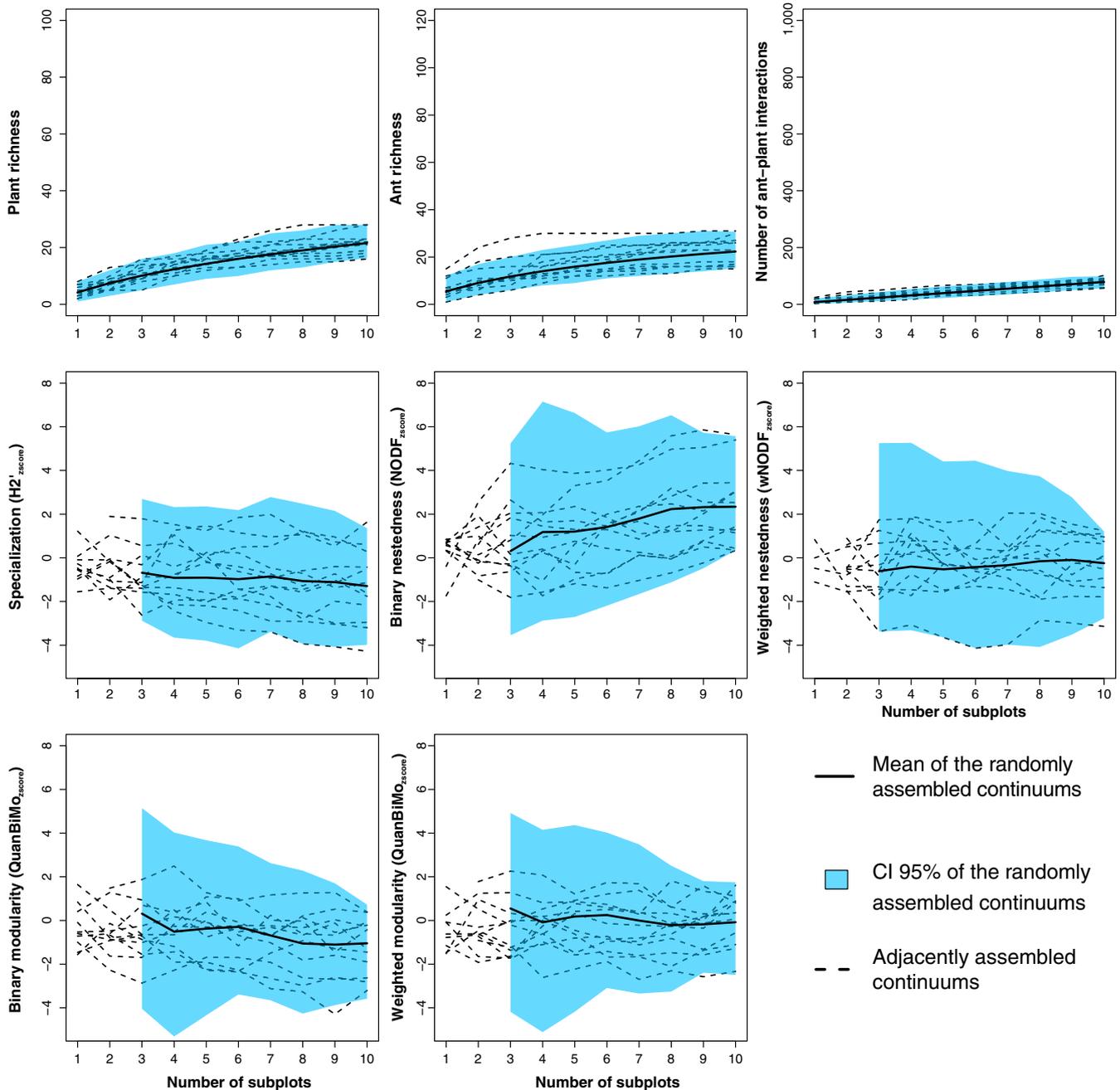
We evaluated the hierarchical arrangement of networks by testing whether species with fewer links and interactions interacted with a subset of the partners of species with more links and interactions (i.e., nested pattern of interactions). For this effort, we estimated binary nestedness using the *NODF* metric (Almeida-Neto, Guimaraes, Guimaraes, Loyola, & Ulrich, 2008). We also estimated the quantitative nestedness based on quantitative matrices called *wNODF* (Almeida-Neto & Ulrich, 2011). Both nestedness metrics vary from zero (not nested) to 100 (perfectly nested). While *NODF* computes the sequence of decreasing marginal totals (i.e., number of links) and the overlap of resources used, *wNODF* considers the same *NODF* principles but weighted by relative frequency (i.e., total interactions; Almeida-Neto & Ulrich, 2011). In other words, rare species may appear specialized in *NODF* since they are not observed very often, while *wNODF* gives a better idea of which species are true specialists by considering the distribution of interactions among partners. Specialization was quantified by  $H_2'$ , an index derived from Shannon entropy based on the deviation between the observed distribution of interactions and the expected distribution of interactions given resource availability. In this specialization index, extreme generalization of an ecological network is  $H_2' = 0$  and extreme specialization is  $H_2' = 1$  (Blüthgen, Menzel, & Blüthgen, 2006). Modularity (*Q*) was calculated with the DIRTLPA+ algorithm, which is known to outperform similar algorithms (Beckett, 2016). Modules are defined as subsets of species that are more highly interlinked among themselves compared to other species in the network. Stochastically, DIRTLPA+ repeatedly divides a network into modules (we set it at  $10^6$  swaps) and recalculates modularity until it reaches an optimal *Q* value, which ranges from 0 to 1 (maximum possible modularity). We calculated both binary (*Q*) and weighted modularity (*wQ*); while the former only considers the presence or absence of interactions, the latter considers the observed frequencies of interactions. As expected, we found that basically all metrics correlated to network size at both spatial scales (see Supporting Information Appendix S1). Therefore, we used null model corrections (z-transformations) to standardize the

difference in the metrics while accounting for variation in species richness, connectance and heterogeneity of interactions between the sampling subplots or plots. This analysis allowed cross-network comparisons (Dalsgaard et al., 2017; Sebastián-González, Dalsgaard, Sandel, & Guimarães, 2015). Values of specialization, nestedness and modularity were standardized as Z-scores, which is defined as:  $Z_{\text{score}} = (x - \mu)/\sigma$ , where  $x$  is the observed value ( $H_2'$ , *NODF*, *wNODF*, *Q* or *wQ*),  $\mu$  is the mean value of randomized matrices, and  $\sigma$  is the standard deviation of the randomized matrices. For each adjacent subplot or plot in both scales, we generated 1,000 random matrices. We used the null model that kept marginal totals to distribute the interactions and produce a set of networks in which all species were randomly associated implemented in the BIPARTITE package in R (Dormann et al., 2009). We used metric means and standard deviations to calculate the Z-scores for both adjacent assembly and random assembly.

In order to evaluate trends of the network structures with increasing sampling scale, each network metric was calculated for each class across the local and regional sampling scales by both random assembly and adjacent assembly. For randomly assembled continuums, we plotted mean values and 95% confidence intervals (all values between the 2.5% and 97.5% quantiles) for both local and regional continuums, while for adjacently assembled continuums, we plotted z-scores for each of the 12 local scale plots and the single regional plot. We calculated the metric sensitivity for increasing sampling scales by evaluating the variation in means and confidence intervals with the accumulation of subplots or plots.

### 3 | RESULTS

We recorded 112 ant species (or morphospecies) of 19 genera and seven subfamilies. Myrmicinae was the most represented subfamily (40.17% of the total ant species,  $n = 45$ ), followed by Formicinae (31.25%,  $n = 35$ ) and Dolichoderinae (13.39%,  $n = 15$ ). Ant species richness per sampling subplot was  $6.75 \pm 4.02$  (mean  $\pm$  standard deviation) and  $23.21 \pm 5.85$  at the regional scale. For the plants, we found 88 species (or morphospecies) that belonged to 41 genera and 26 families within the study area. The family Bignoniaceae comprised 26.3% of plant species, followed by 22.8% Fabaceae: Mimosoideae and 10.5% Fabaceae: Caesalpinioideae. Average plant species richness per sampling subplot was  $4.6 \pm 2.0$  and  $21.4 \pm 3.8$  at the regional scale. Ants and plants engaged in 881 interactions. Overall, the sampling completeness of ant–plant networks varied between scales. At the local sampling scale, we recorded a mean of 72.4% of the plant species (observed: 21 species; estimated: 29 species), 78.5% of the ant species (observed: 22 species; estimated: 28 species) and 82.2% of the expected pairwise interactions (observed: 65 interactions; estimated: 79 interactions). At the regional sampling scale, we recorded a mean of 56.6% of the plant species (observed: 89 species; estimated: 157 species), 52.5% of the ant species (observed: 112 species; estimated: 213 species) and 52.7% of the expected pairwise interactions (observed: 881 interactions; estimated: 1,671 interactions). For



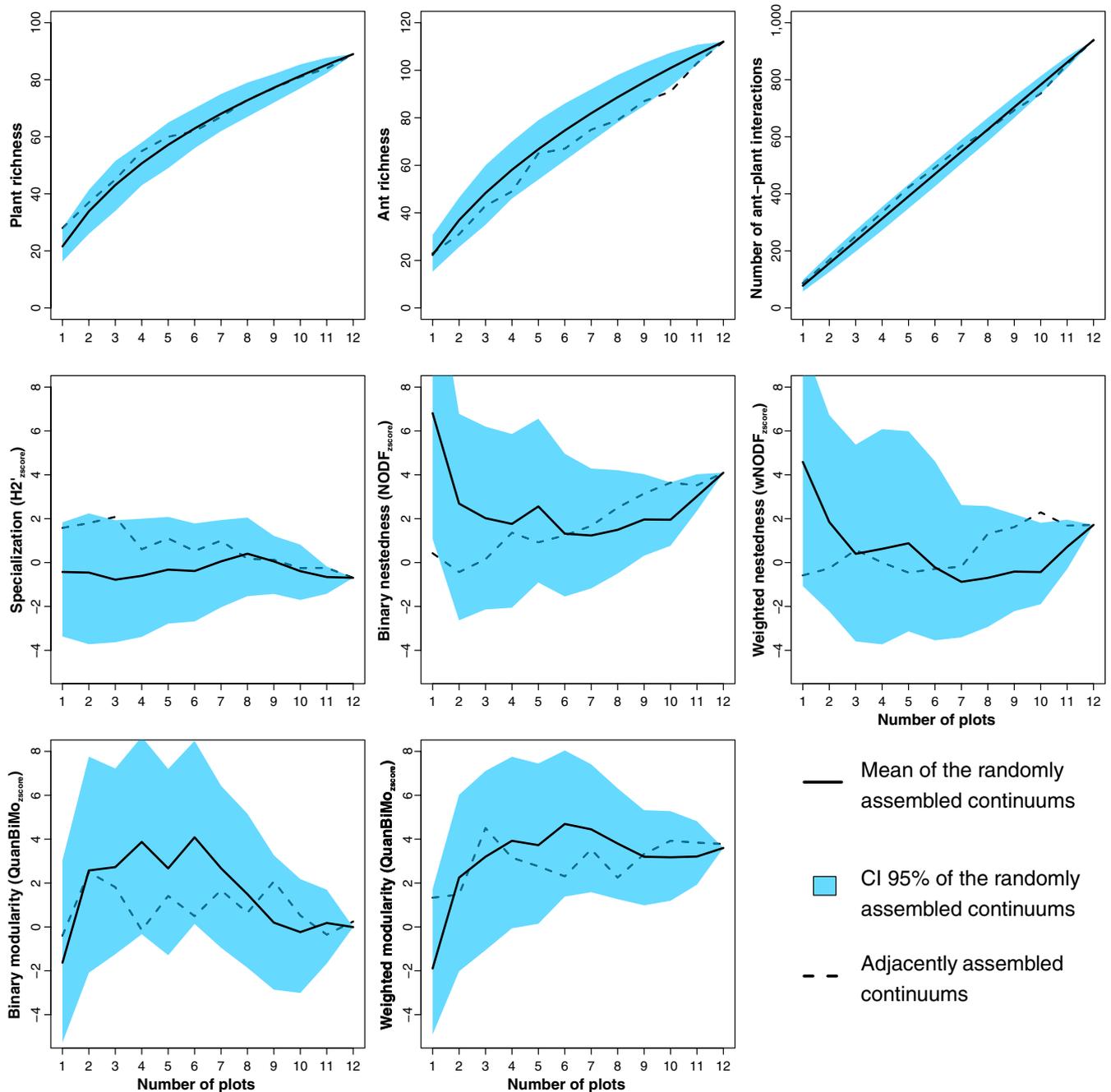
**FIGURE 2** Mean (black line) and 95% confidence interval (shaded area) of the observed network patterns over the expanding local sampling scale by all possible combinations of individual subplots to create increasing spatial continuums. Since the possibilities of randomizations are minimal at the smallest scale networks (i.e.,  $2 \times 2$  species on average), we used the grain size by pooling three subplots. The local continuum gradually increased from 750 m<sup>2</sup> (1 subplot) to 7,500 m<sup>2</sup> (10 subplots). The dashed lines represent the trends obtained for each plot by adding adjacent subplots

both plant and ant composition, we observed that species turnover between plots ( $\beta_2$ ) was higher between plots than between subplots within each plot ( $\beta_1$ ; Supporting Information Appendix S3).

### 3.1 | Trends in network descriptors across the spatial sampling scales

The number of plant and ant species increased with the addition of subplots (Figure 2) and plots (Figure 3), as did the number of

interactions among species. We recorded a higher accumulation rate at the regional compared to the local sampling scale, regardless of adjacent or random subplot or plot addition (compare trends in Figures 2 and 3). However, network descriptors remained fairly constant as sample area increased at the local sampling scale, but were more variable at the regional sampling scale. At the regional scale, nestedness (both binary and weighted) and modularity (binary) substantially varied depending on the order and number of plots added. For weighted modularity, there was an initial steep



**FIGURE 3** Mean (black line) and 95% confidence interval (shaded area) of the network patterns over the expanding regional sampling scale by all possible combinations of individual plots to create increasing spatial continuums. The regional continuum gradually increased from 7,500 m<sup>2</sup> (1 plot) to 90,000 m<sup>2</sup> (12 plots). The dashed line represents the trend obtained by adding adjacent plots

increase following the number of plots added at the regional sampling scale, but their values tended to become constant at around four plots (Figure 3). Interestingly,  $H_2'$  remained relatively constant despite the addition of samples at both spatial scales. Note that we found broad confidence intervals for all metrics at local and regional spatial sampling scales, a result that indicates network descriptors are influenced by which sampling subplots or plots are added. Further, the final value (i.e., when all the plots or subplots were combined at each spatial sampling scale) of most descriptors depended on which plots were considered and how

many subplots were added (Figure 2). Finally, there were no differences in the constancy of network descriptors when subplots or plots were adjacently or randomly combined at both local and regional sampling scales (Figures 2 and 3).

## 4 | DISCUSSION

Our study explicitly evaluated how increasing the extent of spatial sampling from local to regional sampling scales influences the

architecture of ant–plant networks. We observed that, despite the accumulation of species and links with increasing sampling scales, most network descriptors tended to be more constant at local compared to regional sampling scales. Our findings indicate that, in ant–plant interaction networks, species and interactions present local similarity but vary more widely over regional scales. This finding cautions against pooling networks from different plots to describe ant–plant interactions, since they may influence metric values depending on the specific plot considered. Further, we observed that adjacent assembly did not generate more variation in network descriptor values compared to random assembly at the local sampling scale. This finding indicates that the spatially aggregated distribution of species (evidenced in Supporting Information Appendices S2 and S3) and abiotic conditions (Carstensen et al., 2014; Dáttilo, Guimarães, et al., 2013; Trøjelsgaard et al., 2015) does not affect the organization of these interacting assemblages.

Many studies that explored plant–animal networks showed that numbers of species and interactions tend to increase with a greater sampling effort (Dupont & Olesen, 2012; Falcão et al., 2016; Jordano, 2016; Nielsen & Bascompte, 2007). Here, we observed that all descriptors related to network size (i.e., species richness and number of interactions) increased with the addition of subplots (local sampling scale) or plots (regional sampling scale). However, the accumulation curves for these network descriptors were far from reaching stability at the regional scale. Studies revealed the high diversity of plants, ants and interactions among them in tropical environments, even at small spatial sampling scales (Dáttilo & Dyer, 2014), and it is therefore expected that network size may increase substantially with the addition of a spatial sampling scale (more strongly observed at the regional scale). Our findings suggest that the high diversity of ant–plant interactions in primary tropical rainforests may be driven by a high turnover of species and interactions between sampling plots, even over reduced spatial sampling scales. Additionally, we found that most of the utilized metrics were related to network size. Thus, as for other mutualistic systems (Dalsgaard et al., 2017), we suggest the use of null model corrections (e.g., delta and z-transformations) to compare interaction structures across networks while accounting for differences in species richness, connectance and heterogeneity of interactions between the sampling sites (as used in this study). It should be noted that some networks could be extremely small (e.g., two plant species interacting with two ant species), which would hardly be controlled by any correction, since the possibilities for randomizations are minimal (Luna et al., 2017).

On the other hand, we observed that, apart from network size and number of ant–plant interactions, the values of network properties remained similar throughout subplot accumulation at the local sampling scale. The notable constancy of network structure at small spatial sampling scales must be unique for systems where organisms present reduced spatial mobility and life area. In this case, even with the high turnover of species over short distances, the mechanisms that determine the interaction patterns among ants and plants act on small scales. Two key factors that structure ant–plant networks and act at small scales are relative species abundance and

ant dominance hierarchy, where abundant and competitively superior ant species usually tend to interact with a greater number of plant species (Dáttilo, Díaz-Castelazo, & Rico-Gray, 2014; Dáttilo, Sánchez-Galván, et al., 2014; Dáttilo, Marquitti, Guimarães, & Izzo, 2014). Moreover, the central core of highly interacting species (i.e., those species with the greatest number of interactions) remains stable across larger spatial scales in the Brazilian Amazon (Dáttilo, Guimarães, et al., 2013). Consequently, small spatial sampling scales should suffice to record some patterns commonly found in ant–plant interaction networks (as hypothesized in this study), since the high turnover of species over short distances is generated by those peripheral and rare species that are of secondary importance in terms of structuring the networks. On the contrary, the higher species turnover across larger scales (between plots) may explain the greater variation in network structure at the regional scale. It is therefore expected that, for other organism groups like pollinators and seed dispersers, the ability to move over longer distances and the size of their living area could determine the larger spatial sampling scale at which network structure becomes constant (see Burkle & Knight, 2012; Carstensen et al., 2018; Parsche, Fründ, & Tschardtke, 2011). For example, in a few square metres, one can find a highly diverse interactive community of ants and plants. Thus, it is expected that greater proportions of areas would be necessary to result in a constant network structure that involves more mobile organisms. Indeed, modular patterns in plant–hummingbird networks depend on sampling at the landscape scale, since modules emerge from the match of the habitats used by subsets of partners (Maruyama et al., 2014). Moreover, pollination and seed dispersal networks are more strongly constrained by morphological barriers than ant–plant interactions (Vázquez et al., 2009); these barriers create myriad forbidden links in these systems, especially in tropical areas (Jordano, 1987; Vizentin-Bugoni, Maruyama, & Sazima, 2014; Vizentin-Bugoni et al., 2018). Further, we found that most network descriptors calculated from both random assembly and adjacent assembly produced the same deviation from the mean, even with the accumulation of few subplots or plots. This finding indicates that the organization of ant–plant networks is more robust to the inherent spatial variation of ant–plant interactions, since depending on which specific subplot is added, the values of such metrics may not change significantly.

On the other hand, we found substantial variation in the network descriptors depending on the order and number of plots accumulated at the regional sampling scale. The greater variation in network descriptor values at regional scales indicates that regional processes that influence the spatial distribution of ants foraging on plants (e.g., differences in the quantity and quality of resources available among plots) could constitute important mechanisms that shape ant–plant networks (reviewed by Del-Claro et al., 2018). This fact, associated with the frequent rarity (low relative abundance) of most mutualistic species within tropical communities (e.g., Vizentin-Bugoni et al., 2014), indicates that an increased sampling scale is required only at small spatial scales, since pooling multiple networks distributed across large areas may confound with the different environmental drivers of network structures. The differences in sampling

completeness (species and interactions) at local and regional levels indicate that ant–plant networks are highly dynamic over larger spatial sampling scales. Therefore, we recommend the use of sampling completeness to detect whether the structural patterns observed are represented by a large proportion of the species and their interactions within a community. Pooling together multiple regional networks would therefore only be required for continental and global studies, where macroecological factors (biogeography, climate, insularity and latitude) should structure the networks (Trøjelsgaard & Olesen, 2016).

Interestingly, specialization ( $H_2'$ ) was remarkably constant across different spatial sampling scales. This result may occur because there are few constraints to interaction (i.e., forbidden links) between ant–plant pairs. In this case, virtually all of the most important ant species (those with a greater number of interactions) are found everywhere and interact in a similar way (Dáttilo, Guimarães, et al., 2013). Thus, the lack of tight morphological matching of interacting species seems to be constant across populations and scales and leads networks to similar specialization levels since they are independent of the local community composition. In fact, we found low heterogeneity of associations between species based on interaction frequencies (i.e., low specialization) despite the high spatial aggregation of interactions. Moreover, ants do not always forage on the same plant, mainly because the food sources offered by plants are spatially and temporally highly seasonal (Díaz-Castelazo, Rico-Gray, Oliveira, & Cuautle, 2004; Falcão, Dáttilo, & Izzo, 2015), and therefore, the interactions tend to be more generalized (Schoereder, Sobrinho, Madureira, Ribas, & Oliveira, 2010) compared to other specialized ant–plant systems (i.e., ant–myrmecophyte; Dáttilo, 2012) or other mutualisms such as plant–pollinator systems (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007; Maruyama et al., 2014). For this same reason, we did not find that quantitative metrics were less biased by spatial sampling scale than binary metrics (in contrast to findings for pollination networks; Vizenin-Bugoni et al., 2016).

As mentioned by Trøjelsgaard and Olesen (2016), there appears to be considerable invariance in several macroscopic network descriptors (e.g., nestedness and modularity) at small spatial scales, and this phenomenon may occur because biological communities self-organize to increase their robustness to perturbations. However, due to higher turnover of peripheral species across space compared to the few species found in the generalist core (Dáttilo, Guimarães, et al., 2013), microscopic descriptors (e.g., centrality, individual specialization and species roles) tend to vary more across spatial sampling scales (Trøjelsgaard & Olesen, 2016). Additionally, all network descriptors are influenced by the sampling effort via its effects on the record of new ant–plant interactions throughout the year, mainly due to differences in the seasonal phenology of nectaries (Falcão et al., 2016). It therefore appears that most patterns observed in ant–plant networks are more robust to spatial sampling scale variation compared to temporal sampling scales, as demonstrated in this study.

As the main conclusion, we found that local sampling scales generated lower variation in the network descriptors compared to regional sampling scales, and this finding indicates that the processes that effectuate the interaction patterns between ants and plants

could be consistent across local communities. Among all metrics, specialization was the most constant across different spatial sampling scales; this result indicates that the lack of morphological trait matching of interacting species is constant across populations and spatial sampling scales. Our findings have a direct impact on the patterns observed in ant–plant interaction networks, since studies may not be directly comparable without carefully considering spatial sampling designs or analytical standardizations in order to avoid issues related to scale (Dalsgaard et al., 2017; Luna et al., 2017).

## ACKNOWLEDGEMENTS

We greatly appreciate the help of Jéssica Falcão with the fieldwork and the staff of the Central Herbarium of Universidade Federal de Mato Grosso (Brazil) for identification of plant specimens. We thank Reuber Antoniazzi for his help in calculating beta diversity. This work has been supported by grants from the Office National des Forêts Brazil and the Brazilian Research Program in Biodiversity (PPBio Project) (CNPq no. 558225/2009–8). This is publication 100 in the Núcleo de Estudos da Biodiversidade da Amazônia Mato-Grossense technical series. Financial support to J.V.-B. was provided by CAPES through a Ph.D scholarship and by CERL-ERDC through a postdoctoral grant. P.J. acknowledges Spanish MINECO CGL2013-47429P, a Severo Ochoa Excellence Award (SEV-2012-0262) and a Junta de Andalucía Excellence Grant (RNM-5731) for support. T.J.I. thanks Conselho Nacional de Pesquisas (CNPq – 479243/2012–3).

## AUTHORS' CONTRIBUTIONS

W.D., P.J. and T.J.I. conceived the ideas and designed the methodology; W.D. collected the data; W.D., J.V.-B. and V.J.D. analysed the data; and all authors wrote the manuscript and approved the final version.

## DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.hk5n4m1> (Dáttilo, Vizenin-Bugon, Debastian, Jordano, & Izzo, 2019).

## ORCID

Wesley Dáttilo  <https://orcid.org/0000-0002-4758-4379>

Jeferson Vizenin-Bugoni  <https://orcid.org/0000-0002-6343-3650>

Pedro Jordano  <https://orcid.org/0000-0003-2142-9116>

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## SUPPORTING INFORMATION

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

**How to cite this article:** Dáttilo W, Vizentin-Bugoni J, Debastiani VJ, Jordano P, Izzo TJ. The influence of spatial sampling scales on ant–plant interaction network architecture. *J Anim Ecol*. 2019;88:903–914. <https://doi.org/10.1111/1365-2656.12978>