RESEARCH ARTICLE

Sampling bias in multiscale ant diversity responses to landscape composition in a human-disturbed rainforest

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Abstract
Recent studies have shown that several sources of variation can influence our ability to quantify biological responses to environmental variables, and that spatial scales are important in this process. For instance, sampling methods may differ in their efficiency or specificity, leading to different inferred relationships between community responses and landscape composition—i.e., forest cover (%), landscape heterogeneity, edge effects, and functional connectivity. Consequently, this can also influence the predictive power of the models when evaluating organisms as bioindicators of habitat loss and land use modification. Here, we evaluated how sampling methods (i.e., Winkler, pitfall, beating, and baits) influence our capacity to assess the scale of effect of two landscape composition metrics on ant diversity. We conducted ant sampling in 16 landscapes within a Mexican tropical rainforest and assessed the relationship between species richness and landscape composition metrics through buffers with 12 different spatial extents (from 50 to 1000 m). We found that the sampling method influenced the scale of effect when evaluating the relationships between ant species richness and forest cover and landscape heterogeneity. Combining all sampling methods, we found that the scales that best explained ant species richness were 700 m for forest cover and 900 m for landscape heterogeneity. Therefore, we highlight that our ability to detect ant-based diversity responses to environmental variables depends on the sampling method and spatial extent used in the study.

Keywords Forest cover · Formicidae · Landscape heterogeneity · Sampling method · Spatial extent

Introduction

Habitat destruction and land use change are some of the main drivers of biodiversity decline and species extinctions worldwide (De Chazal and Rounsevell 2009; Cardinale et al. 2012). These changes in the environment generate variation in landscape composition and configuration, such as decreasing the amount of habitat, increasing patch isolation, edge effects, and spatial heterogeneity, thus altering the spatial reorganization of diversity in fragmented landscapes (Falcucci et al. 2007; Fletcher and Fortin 2018). Therefore, knowing the spatial scale at which organisms respond to the local and surrounding environment that characterizes their habitat could improve our understanding of the spatial patterns of organism distribution in a changing world (Levin 1992; Crouzeilles and Curran 2016; Miguet et al. 2017).

One way to understand how species respond to environmental variation at the landscape level is to assess the spatial extent with the strongest influence on ecological responses (Jackson and Fahrig 2012; Miguet et al. 2016). Some studies have shown that the selection of the landscape variables and biological responses to be evaluated for such scale of effect can substantially influence our capacity to detect environmental gradient effects, since many of the studies can be context dependent (i.e., when the sign and/or magnitude changes as a function of the biotic or abiotic context) and, therefore, results are not comparable with other biological

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groups (Miguet et al. 2016; Egerer et al. 2017; Martin 2018; Moraga et al. 2019). It is well documented in the literature that various ant sampling methods each collect a different spectrum of fauna and, thus, some components of the ant fauna may be overrepresented by some methods (Longino et al. 2002; Missa et al. 2009). As such, sampling methods differ in their efficiency and specificity in capturing certain organisms depending on their biological size and natural history (Mahon et al. 2017); this topic has often been neglected in the literature dealing with the scale of effect—i.e., the spatial extents that best explain the patterns encountered. Thus, it is necessary to evaluate if the variation in species richness produced by different sampling methods influences our ability to understand the scale of effect of spatial patterns of biodiversity.

Given their sensitivity to habitat change and environmental disturbance, ants are widely used as a bioindicator group to study the effects of habitat loss and fragmentation (Crist 2009; De la Mora et al. 2013; Ahuatzin et al. 2019). Because ants have a broad spectrum of feeding and nesting behaviors, occupy different microhabitats, and are associated with numerous species of plants and animals (Beattie and Hughes 2002; Ryder-Wilkie et al. 2010; Montine et al. 2014; DaRocha et al. 2016; Fagundes et al. 2018; Plowman et al. 2020), various sampling methods have been developed to record the largest number of ant species at the community level (Bestelmeyer et al. 2000). These methods can be passive (e.g., pitfall, baiting) or active, such as directed searches for study organisms and colonies or manual collection (e.g., vegetation beating and Winkler extractor) (Bestelmeyer et al. 2000; Mahon et al. 2017). Both active and passive sampling methods have advantages and disadvantages, generating bias when capturing ants. For instance, passive methods depend on the differences in the activity and behavior of ant species; therefore, we do not make a real estimate of ant abundance, but rather activity density. On the other hand, active methods depend on the detectability of organisms and the collector's ability (Bestelmeyer et al. 2000; Mahon et al. 2017). Additionally, most common standardized ant-capture methods target different ant guilds: whereas pitfall traps are useful for collecting ants that are active on the ground surface as well as some epigeic fauna (Torres et al. 2020), Winkler extractors are used to collect ants inhabiting the leaf litter, while surface baiting captures ground-foraging ants (Agosti and Alonso 2000). For these reasons, ants are an excellent group with which to assess sampling bias in multiscale responses to landscape composition (Andersen et al. 2002; Carvalho et al. 2020).

As for other taxa, the response of ant communities to environmental variation is scale dependent (Andersen 1997), as processes and parameters important at one scale may not be as important or predictive at another scale (Turner 1989). For example, forest cover in a 500 m radius explains ground-dwelling ant species richness in a sandhill habitat (Spiesman and Cumming 2008), while forest cover in a 200 m radius contributed to the prediction of the richness of twig-nesting and leaf litter ants within agricultural landscapes (De la Mora et al. 2013). However, although the increasing number of studies on multiscale ant responses to forest cover have established the importance of the scale of effect, other landscape features, such as spatial heterogeneity (Fahrig 2013; Klingbeil and Willing 2016), remain to be elucidated in detail. Moreover, multiscale studies of the ant community have produced contradictory conclusions about the biologically relevant scale of the effect for these organisms, and this can be attributed to the use of different sampling methods and the analysis of different (or even limited) spatial extents (Spiesman and Cumming 2008; De la Mora et al. 2013; Egerer et al. 2017; Reynolds et al. 2017; McCary et al. 2018).

Here, we aimed to answer two main research questions: (i) How does the spatial extent of the study influence the effect of landscape composition (i.e., forest cover and landscape heterogeneity) on ant species richness? (ii) How do sampling methods influence the assessment of ant–landscape associations across different spatial extents? We predicted that: (i) landscape composition extents will have more influence on ant species richness at a small spatial scale than at a large spatial scale, as several ant species have small home ranges and depend strongly on the microenvironmental conditions given by forest cover and changes in the vegetation of the surrounding habitat (Katayama et al. 2014) and, based on the evidence that different sampling methods capture different species compositions (e.g., cryptic, epigeic, and arboreal), (ii) information regarding the species present generated via each sampling method or combination of methods would generate differences in the biological response of the species to the study scale. Specifically, we expected that methods that capture mostly habitat specialists and less mobile ants (Winkler extractor and beating) would be sensitive to responses at small spatial extents, while the scale of effect should be larger when methods that capture more generalist and mobile species (pitfall and baits) are employed, since heterogeneous landscapes can favor the presence of habitat generalist species (Dunning et al. 1992; Neves et al. 2020).

Methods

Study site

We conducted this study in the Los Tuxtlas Biosphere Reserve, located in the coastal plain of the Gulf of Mexico, in the southeast of the State of Veracruz (18°30′ to 18°40′N and 95°03′ to 95°10′W), covering a total area of 155,122 ha (Von Thaden et al. 2018). According to the Köppen climatic

classification, the climate is humid and warm throughout the year (Af), with average annual precipitation of more than 4000 mm and average annual temperature of 27 °C (Soto 2006). The dominant vegetation is tropical rainforest (Von Thaden et al. 2018). In the last decades, the original vegetation has been converted into agricultural fields and pastures, leaving native vegetation remnants in different conservation states immersed in an anthropogenic matrix (Vega-Vela et al. 2018; Von Thaden et al. 2018) (Fig. 1).

Landscape selection

The samplings were conducted in 16 landscape units, which were selected to represent a gradient of forest cover and spatial heterogeneity. This number of landscapes has been demonstrated to be enough to detect relationships between landscape structure and ant biological responses in a previous study in the same landscapes (Corro et al. 2019) and in a fragmented landscape in southeastern Brazil (Martello et al. 2016; Lasmar et al. 2021). Each landscape unit had a sampling point in a primary forest fragment (except for landscapes with 0% primary forest cover, where sampling

points were located in secondary forest). We used high-resolution multispectral (QuickBird: 2.4 m resolution) and panchromatic (resolution of 0.6 m) images obtained in October 2014 to characterize landscape structure. Initially, we performed a validated supervised classification with 200 training points in the field. Using IDRISI® software (Eastman 2001) in vector format (i.e., shapefile), we utilized the moderate classifiers BAYCLASS and BELCLASS, which determine the probability of a pixel belonging to one of the landscape classes. Likewise, the HARDEN and BAYCLASS modules were used to perform a classification that consists of assigning each pixel of the image to a single category. The classification allowed us to generate a map of land use covers using the main categories in the study region according to Vázquez et al. (2010) and Castillo-Campos et al. (2011): (i) primary forest, (ii) secondary forest, (iii) riparian forest, (iv) live fences, (v) pastures, (vi) crops, (vii) sand, (viii) urban area, (ix) road, and (x) water (Supp. Table 1). Subsequently, we converted our vector map to raster format (cell size 2 m) in the ArcGIS program version 10.2.2. For each of the 16 landscape units, we marked a central point (centroid) from which 12 buffers with different spatial extents were
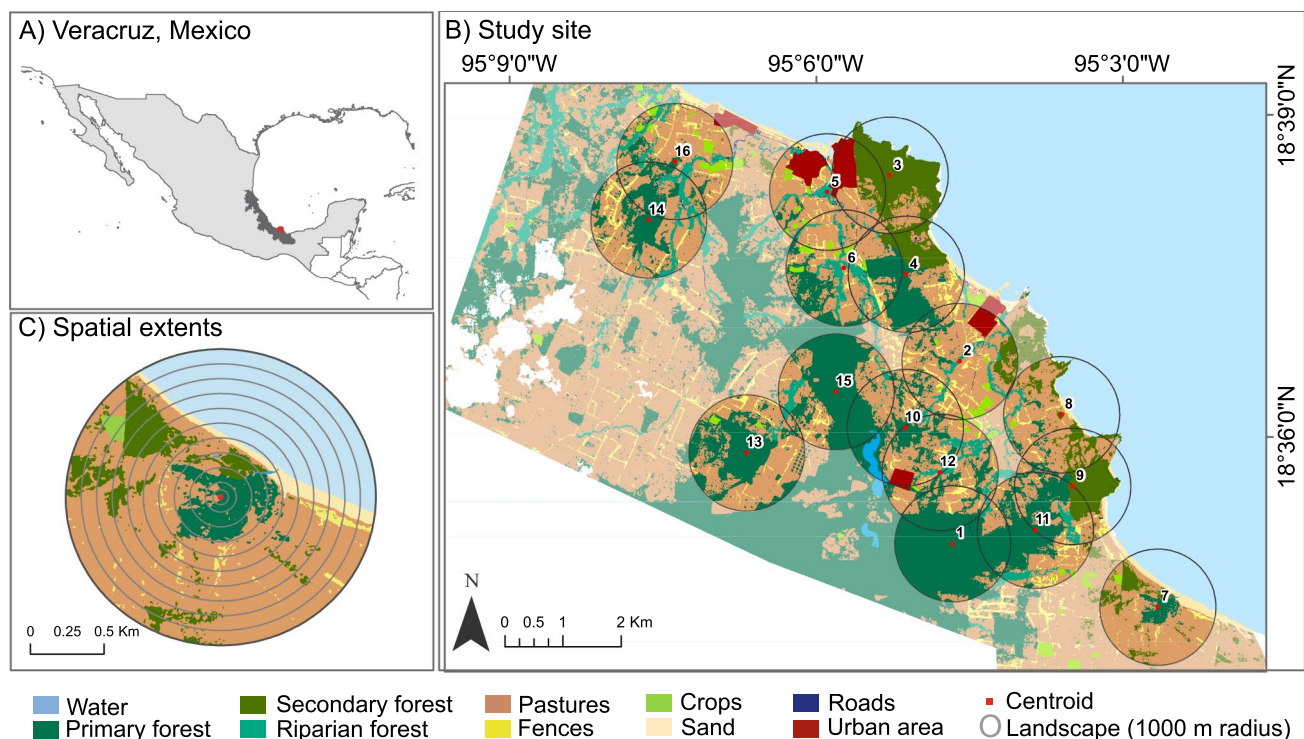

Fig. 1 **A** Location of the 16 sampling landscapes and **B** land use cover classifications associated with Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. Each sampling landscape had a centroid, from which we generated buffers with 12 different spatial extents to perform the multiscale analysis. As an example, landscapes of 1000 m radius are shown in panel **B** of the map. **C** Example of buffers generated from the centroid of Sampling Landscape (#7), where each buffer represents a different spatial extent of the study area (50, 100, 150, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 m)

delimited: 50, 100, 150, 200, 300, 400, 500, 600, 700, 800, 900, and 1000 m. The landscape metrics were calculated for each landscape and for each spatial extent.

To find the biologically relevant spatial extent (scale of effect) that best explains ant species richness at the landscape level, we followed the proposal of Jackson and Fahrig (2012), who indicated that the radius of a landscape should be 0.3–0.5 times the maximum dispersal distance of the organisms. The smallest buffer size (radius = 50 m) for analysis is subject to stronger influence from local environmental factors that operate in a smaller spatial extent (e.g., microclimate and local resources availability) and can be associated with canopy cover, vegetation structure, and leaf litter (De la Mora et al. 2013; Solar et al. 2016). At the other extreme, the dispersal flight of reproductive adults and data regarding some genera of ants that occur in the study area (*Azteca* spp. = 400 m, *Pheidole* spp. = 30 m) (Helms 2018) established the maximum spatial extension at 1000 m. Note that our landscape units presented overlap in the spatial extension of 1000 m (overlap between two units independent of other sampled landscapes = 8.46% ± 1.64%. Mean ± SE). According to Zuckerberg et al. (2012), a greater overlap does not necessarily violate the statistical independence of landscapes, especially when the spatial overlap is small (as in our study).

To evaluate the scale of effect on ant species richness (i.e., the number of collected species), we selected primary forest cover (in %; hereafter forest cover) and landscape heterogeneity to characterize landscape structure. Both variables are a proxy that allow us to evaluate how environmental variability can modulate species richness in the landscape (Christianson and Kaufman 2016). Additionally, these descriptors have been the main components used to characterize human-modified landscapes (Fahrig et al. 2011; Martensen et al. 2012; Corro et al. 2019). Primary forest was defined as forest land cover with native tree species, in which there is no evidence of human activity and ecological processes are not significantly disturbed (Kelatwang and Garzuglia 2006). For the purpose of our study, the land use and land cover maps were reclassified as binary maps: forest (1) and matrix (0), in which the class of matrix included all other types of land cover, regardless of whether they are natural or anthropogenic. Using the binary maps as input, we calculated the forest cover (%) for each landscape and for each spatial extent. Landscape heterogeneity was measured using the exponential of Shannon's index (Shannon and Weaver 1949), which quantifies landscape diversity based on two components: the number of landscape classes (i.e., land cover type) and the variance in the proportion of the area covered by each class type. In human-dominated landscape units, high landscape heterogeneity could be an indicator of high disturbance and environmental variability (Fahrig et al. 2011), given by the high number of land cover types (heavily

degraded pastures and secondary forests) surrounding the primary forest fragments (see Fig. 1). We calculated both metrics for each sampling unit (i.e., landscape) using the *raster* version 2.9–5 (Hijmans et al. 2019), *SDMTools* version 1.1-221.1 (Van Der Wal et al. 2019), and *vegan* packages (Oksanen et al. 2017) of the statistical program R (R Core Team 2021). The sampling unit characterization indicated that there was a change in forest cover and landscape heterogeneity as spatial extent increased. The average forest cover decreased by half as the spatial extent increased (percentage of average initial forest at 50 m = 52.5% ± 12.12 SE, final average forest percentage at 1000 m = 26.6% ± 5.35 SE) (Supp. Fig. 1a). Landscape heterogeneity showed the opposite pattern, increasing as spatial extent increased (initial mean heterogeneity at 50 m = 1.26 ± 0.09 SE, final average heterogeneity at 1000 m = 3.7 ± 0.23 SE) (Supp. Fig. 1b).

Ant sampling

To obtain a representative sample of ant species from a wide range of microhabitats and foraging habits, we used different sampling methods for soil (Winkler extractor, pitfall, and bait) and vegetation (beating) (Tista and Fiedler 2011). Samplings were carried out during the dry season (Guevara et al. 1994), in April and May 2016, between 10:00 and 15:00 h. Sampling was performed at the centroid of each landscape unit (Supp. Fig. 2). Since each centroid was located within primary forest fragments of varying sizes, we placed transects and quadrants close to the centroid in landscapes with high primary forest cover (> 50%), whereas, for landscapes with low forest cover (< 50%), sampling was carried out by selecting a random point near the centroid. Transects were placed parallel to each other at 10 m intervals.

To collect ants using the Winkler extractor, we established a 50 m transect in the center of each landscape (Supp. Fig. 2). Every 10 m, a 1 m^2 leaf litter sample was taken of the upper layer of the forest soil and sieved before being placed in the Winkler extractor for 48 h ($n = 5$ traps per landscape unit) (Sobrinho and Schoereder 2007). This method allowed the capture of dominant and common ants, as well as registering small and cryptic species that live in the litter and in the upper layers of the soil that are not normally captured by other methods (Bestelmeyer et al. 2000; Silva et al. 2013; Wiezik et al. 2015). To collect using the pitfall method, we established another 50 m transect (Supp. Fig. 2) and installed a pitfall trap (without bait) every 10 m for a 48-h period ($n = 5$ traps per landscape unit). The trap consisted of a 1 L plastic container buried at ground level (110 mm diameter × 150 mm depth), to which 200 mL of a solution of water, detergent, and salt was added to preserve the captured organisms and prevent individuals from escaping. Pitfall traps enable continuous collection of epigeal species during the day and night,

over longer time intervals than provided by other methods (Greenslade 1973; Gotelli and Colwell 2001; Borgelt and New 2005).

To collect ants using bait, we established two 70 m transects and placed traps with two types of attractants (tuna and honey) (Supp. Fig. 2). The baits were placed in the center of a plastic card (9×6 cm) and exposed for 2 h on the surface of the soil to avoid competitive exclusion (i.e., a dominant species spatially excluding a subordinate one through its presence) (Parr 2008). After 2 h of exposure, we collected all the individuals and only recorded the incidence of each species per trap for subsequent analyses ($n = 16$ baits per landscape unit, comprising eight tuna baits and eight honey baits placed alternately). This method attracts ants with mostly generalist habits (Bestelmeyer et al. 2000; Hahn and Wheeler 2002). We increased the number of baits per transect in comparison to pitfall traps and Winkler extractors, because, in landscapes with a large percentage of pastures, there is high disturbance generated by farm animals and samples can be lost, resulting in a tendency to capture fewer ants as seen in Wang et al. (2001). However, no bait was lost in any landscape unit studied.

Additionally, we made a quadrant of 50×40 m to collect ants that forage in the vegetation using the beating method. This method consisted of choosing a focal plant higher than 0.5 m and less than 3 m (accessible to the collector); then, a 1 m^2 blanket was placed under the branches, the foliage was shaken, and the ants that fell on the blanket were collected (Dáttilo and Dyer 2014; Falcão et al. 2015). Sampling was started by collecting specimens from the first plant in a corner of the quadrant, followed by a plant every 10 m until the edge of the quadrant, allowing us to minimize overestimation of the abundance of species with high recruitment, as well as the effect of the proximity of the nests ($n = 25$ plants per landscape unit) (Miranda et al. 2019). The spatial arrangement of the plants consisted of a grid in which each plant was separated from the others by at least 10 m and considered an independent sample unit (Supp. Fig. 2). In other words, we assumed that, for most ant species, the distance between plants was sufficient to guarantee that the ants of a given nest would have little chance of foraging on two different plants. These data were previously collected by Corro et al. (2019), in whose report one can find detailed information about ants that forage in the vegetation.

All collected samples were fixed in 70% ethanol and processed for subsequent identification. We considered the updated list of the myrmecofauna of the Biological Station Los Tuxtlas as a reference for the study system (Longino et al. 2017; Dáttilo et al. 2020). Then, taxonomic determination was carried out at the species level with morphological comparisons of the species present in the Entomological Collection of the Instituto de Ecología A.C. (IEXA), where the specimens were deposited.

Data analysis

We estimated the completeness of the ant species inventory using the sample coverage considering the total abundance (incidence per trap) obtained by each sampling method (Winkler, pitfall, beating, and baits) individually, and then considering all methods in the 16 landscape units (Winkler = 80 traps, pitfall = 80 traps, vegetation = 400 plants, and baits = 256 traps) using the *iNEXT* package version 2.0.12 (Hsieh et al. 2016. The sample coverage represents the proportion of individuals of the species collected in the sample (Chao and Jost 2012). When the estimator is close to 100%, it can be concluded that sampling has been completed, depending on the sampling effort and method (Chao and Jost 2012). It is important to highlight that, although there is a difference in the sampling effort between the sampling methods, sample coverage showed that the individual methods had completeness from 92% to 98% (see Results) and, therefore, are comparable. Likewise, we obtained the expected values of richness when analyzing the combined use of capture methods as well as each individual method type, considering the maximum sample size ($n = 2545$ total incidents) and the 95% confidence interval (Hsieh et al. 2016). We used the *vegan* package to estimate the completeness of the inventory (Oksanen et al. 2017). All data analysis was performed using the software R (R Core Team 2021).

We evaluated the relationships between forest cover and landscape heterogeneity (as explanatory variables) and ant species richness (as the response variable) using generalized linear models (GLMs) at the 12 different spatial extents. We performed the analyses for each landscape variable and method (for each single method and combinations of two methods, three methods and all the methods). Partial residual plots were used to verify potential residual analysis problems in GLM analyses, and data transformations were not needed. Due to the nature of the response variable, for species richness (q^0), a Poisson error distribution was employed (Guisan et al. 2002). We evaluated a total of 360 models for forest cover and 360 models for landscape heterogeneity. Following the method proposed by Jackson and Fahrig (2015), we calculated the coefficients of determination (R^2) between richness and landscape variables (forest cover and heterogeneity) to identify the spatial extent that best predicted ant species richness (i.e., scale of effect). To obtain comparable coefficients of determination, we standardized the landscape variables (forest cover and landscape heterogeneity) by the maximum value of each (standardized variables have values between 0 and 1) (Solar et al. 2016). All GLMs were performed using R software (R Core Team 2021).

Finally, we used Moran's index (Moran's *I*) in the *ape* package in R (Paradis et al. 2021) to evaluate the presence of spatial autocorrelation in the data and the results

of forest cover and landscape heterogeneity at a scale of 1000 m. Moran's *I* values range from −1 to +1, representing even dispersion and clumped dispersion, respectively; the expected value is very close to 0 under a complete spatial randomness hypothesis. We found no evidence of positive spatial autocorrelation (i.e., spatial clustering) at a scale of 1000 m with regard to either forest cover (Moran's $I = 0.02$, $P = 0.10$) or landscape heterogeneity (Moran's $I = −0.06$, $P = 0.49$), indicating spatial and statistical independence for our landscape units.

Results

Species richness and community composition

Taking into consideration all four sampling methods, we recorded 197 ant species distributed in 51 genera and 10 subfamilies. Myrmicinae comprised the highest number of genera ($n = 27$ genera, 53% of the total recorded) and species ($n = 120$ species, 61% of the total recorded). The most representative and abundant genus was *Pheidole* (30% of the total species recorded, $n = 59$ species and morphospecies, with 443 records including all methods), followed by *Camponotus* (8%, $n = 15$ species and morphospecies, 287 records) and *Pseudomyrmex* (5%, $n = 9$ species, 286 records). The most frequent ant species recorded were *Camponotus planatus* (123 records, 6% of the total), *Wasmannia auropunctata* (6%, 123 records), and *Pseudomyrmex salvini* (5%, 103 records). The method that captured the highest species richness ($n = 93$ species) was the Winkler extractor, while the beating method captured the lowest number of species ($n = 50$ species). Based on analysis of the sample coverage for both the total and each type of sampling method, we found a completeness > 92% (range of sampling deficit 8% to 2%, Supp. Table 2), indicating that we had a representative sample of the ant fauna in the study area and that each method captured a fraction of the total species (Supp. Fig. 3).

Only nine species were shared among all the methods (~5% of the total species). In fact, we recorded several species that were collected only by a single method: Winkler extractor = 54 unique species, pitfall = 28 species, baits = 35 species, and beating = 23 species. From the Winkler extractor, the most common species were *Solenopsis* sp. 1 (10% of total occurrences for the Winkler extractor), *W. auropunctata* (8% of occurrences), and *Octostruma trithrix* (5% of occurrences). Using the pitfall method, the most common species were *W. auropunctata* (8% of the total occurrences for pitfall), *Solenopsis* sp. 1 (6% of occurrences), and *Pachycondyla harpax* (5% of occurrences). For baits, the most recorded species were *W. auropunctata* (12% of total occurrences for baits), *Solenopsis geminata* (6%), and *Pheidole* sp.

6 (6%), while for the beating method they were *C. plantatus* (15% of the total occurrences for beating), *P. salvini* (11% of occurrences), and *Dolichoderus bispinosus* (11% of occurrences) (Supp. Table 3).

Multiscale responses of species richness

We found that there was a range of different scales of effect, depending on the sampling method used to evaluate ant species richness and landscape variable analyzed. When all the sampling methods were combined, we found that the scale of effect that best explained the variation in ant species richness as a function of forest cover was observed at the spatial extent of 700 m ($R^2 = 0.18$, $p = 0.01$). Most of the sampling methods used did not show a relationship between ant species richness and forest cover. However, the Winkler extractor showed a relationship between ant species richness and forest cover over a wide range of spatial extensions and had the highest coefficient of determination at the spatial extent of 300 m ($R^2 = 0.26$, $p < 0.05$). Combinations of two or three methods which included Winkler extractor data also showed a relationship with primary forest cover (Fig. 2, Supp. Table 4).

When considering landscape heterogeneity, we found that the scale of effect on ant species richness also showed different responses for each sampling method. For all sampling methods, we found that the scale of effect was at a spatial extent of 900 m ($R^2 = 0.25$, $p = 0.002$) (Fig. 3). Similar to the results found for forest cover, only the Winkler extractor showed a relationship between richness and landscape heterogeneity, with a scale of effect in the spatial extent of 900 m ($R^2 = 0.25$, $p < 0.05$), while combinations of two or three methods including Winkler extractor information showed a relationship with landscape heterogeneity (Fig. 3, Supp. Table 4).

Discussion

We found that ant sampling method influenced the scale of effect when evaluating the relationship between ant species richness and landscape composition in a fragmented Mexican tropical rainforest. We observed that each sampling method collected a fraction of the overall myrmecofauna, which strongly can influenced ant species richness (Missa et al. 2009). Moreover, analysis of ant species richness responses considering all sampling methods together indicated that forest cover and landscape heterogeneity influenced our response variables over a wide range of spatial extents. However, we observed that only combinations of two or three methods, where Winkler extractor richness was included, showed a relationship with the landscape metrics evaluated. Our results suggest that the scale of effect at
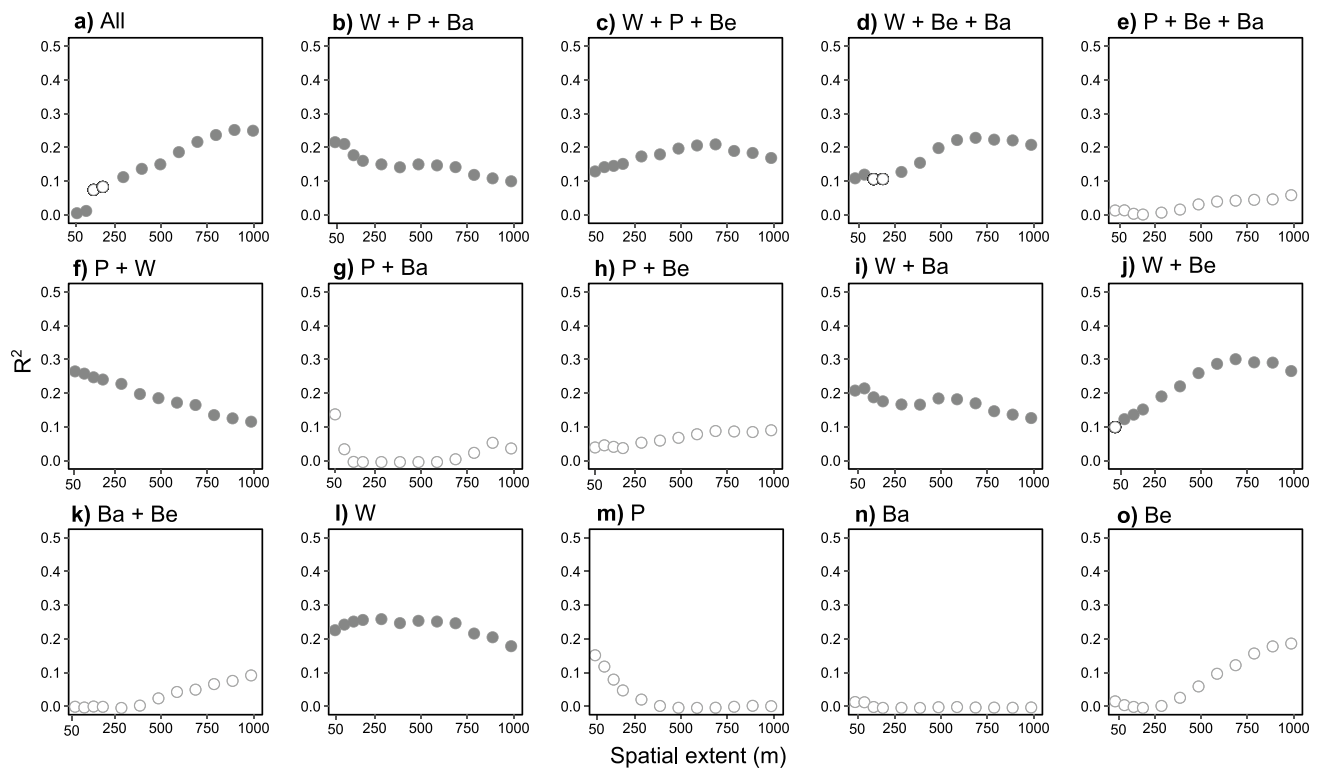
Fig. 2 Effect of forest cover (%) on species richness at 12 spatial extents (50–1000 m). The scale of effect is the spatial extent with the highest R^2. **a** Combination of all ant sampling methods: Winkler extractor (W), pitfall (P), baits (Ba), and beating (Be). **b–e** Combinations of three methods. **e–k** Combinations that include only two sampling methods. **l–o** Individual methods. The white points and solid points indicate statistically non-significant and significant coefficients, respectively, of the evaluated models in each spatial extent

which ant species richness response is influenced by landscape composition depends not only on the landscape variables evaluated and type of biological metric used (Miguet et al. 2016; Martin 2018), but also the sampling method.

In this study, we used various sampling methods to characterize the ant community structure of a tropical rainforest and, as expected, found that none of the methods used captured all the registered species for all the landscape units. Such results echo those reported by Salata et al. (2020), who indicated that species richness varies with the sampling method. Additionally, Missa et al. (2009) compared the suitability of four sampling methods to monitor arthropods in a tropical landscape (pitfall, Malaise, flight interception, and yellow pan traps). They found that each sampling method was biased toward specific taxa and morphospecies (Missa et al. 2009). This could indicate that each sampling method underestimates information for the ant species richness present in each landscape unit of our study area. King and Porter (2005) observed that sampling design, including sampling method types, as well as some spatial limitations (i.e., number of samples), were more important factors than sampling effort in measuring differences in ant species. It is important to emphasize that it is not always essential to obtain the highest number of species in each area

to detect the biological patterns (or effects) that researchers are interested in. In the current study, Winkler extractor collected most of the species in the study area and was the only method found to be useful for detecting the effect of forest cover (%) and landscape heterogeneity on ants. For this reason, it is important to consider that data collected with different methods can lead to inappropriate inferences about ant diversity (Salata et al. 2020).

Different sampling methods can generate lists of different and/or complementary species, resulting in conflicting data regarding ant species richness (Fisher 1999; Lopes and Vasconcelos 2008; King and Porter 2005; Souza et al. 2012). In fact, sampling methods may function as a filter, where each method captures certain species depending on their habitat preferences or morphological traits (Lee and Guénard 2019). For example, we recorded the highest number of species using the Winkler extractor, which represented mainly a trophic guild of small cryptic species with high specificity for certain microclimatic conditions (Lee and Guénard 2019). Meanwhile, the other methods, such as beating and baits, captured larger organisms with other, mostly general habitat specificities (and possibly because of that showed no multiscale response of species richness to landscape composition, independent of analyzed spatial scale). One of the
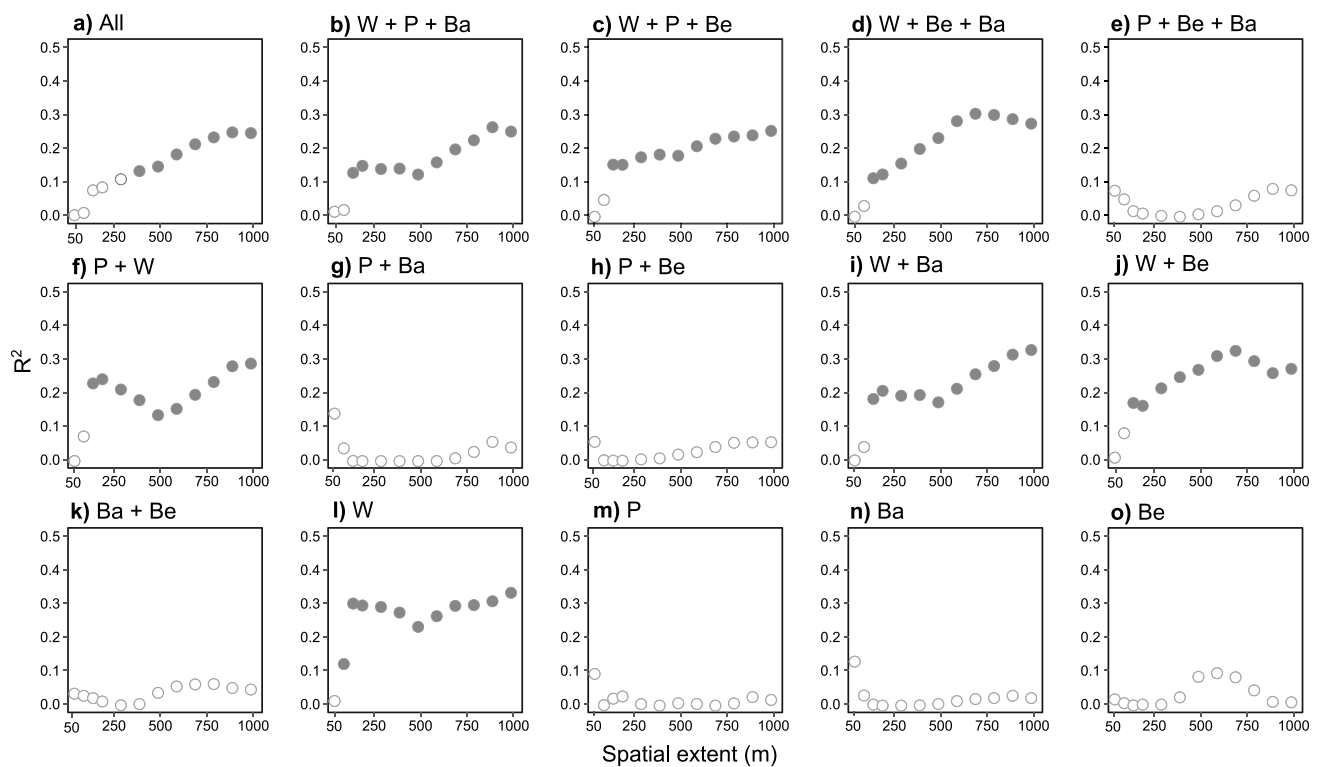
Fig. 3 Effect of landscape heterogeneity on species richness in 12 spatial extents (50–1000 m). The scale of effect is the spatial extent with the highest R^2. **a** Combination of all ant sampling methods: Winkler extractor (W), pitfall (P), baits (Ba), and beating (Be). **b–e** Combinations of three methods. **f–k** Combinations that include only two sampling methods. **l–o** Individual methods. The white points and solid points indicate statistically non-significant and significant coefficients, respectively, of the evaluated models in each spatial extent

limitations of this study was that we did not collect canopy ants, which are a dominant group in the treetops of our study region with different nesting and foraging behaviors (Antoniazzi et al. 2021a, b). Therefore, we recommend the use of different and complementary methods (e.g., arboreal pitfall traps and hand collecting) to evaluate sampling bias in multi-scale responses of canopy ant diversity to landscape composition (Tiesta and Fiedler 2011; Silva et al. 2013; Antoniazzi et al. 2020). Moreover, if the influence of landscape composition on ant community structure is analyzed using only a single method, the results would represent only the ecological response of the few trophic guilds that this method captures. On one hand, it is possible that more mobile ants experience broader microenvironmental variation and are more resilient to habitat loss and land use change. On the other hand, the most cryptic ants tend to be more sensitive to landscape changes, as they do not have contact with a wide range of microclimate variation (Hoffmann and Andersen 2003). In this way, the fauna collected by Winkler extractor seems to respond better to variations in this spatial scale. Therefore, the choice of sampling method can be a potential source of error in evaluating species' response to landscape structure, as multiple methods show differences in the scale of effect (Churchill and Arthur 1999; Melbourne 1999).

Ant species interact with biotic and abiotic factors at different scales and these interactions are based on their inherent habitat specialization, dispersal ability, body size, resource requirements, and other life history traits (Steffan-Dewenter et al. 2002; Miguet et al. 2016; Reynolds et al. 2017; Fernandes et al. 2020). For instance, Holland et al. (2004) evaluated forest cover in a region of Ontario, Canada, and showed that species of long-horned beetles (Cerambycidae) responded to the landscape in different spatial extents, suggesting that some landscape variables are more important at one range of scales than they are at others. Consequently, habitat variables (i.e., forest proportion) may influence the beetles to select habitat at a fine scale, while the availability of habitats on a large scale can limit the areas within which a beetle species can occur. In this study, although both landscape compositional variables—forest cover and landscape heterogeneity—seemed to have a similar scale of effect, they showed a relationship with ant species richness at a wide range of scales. This seems to indicate that both variables are important to explain ant species richness, since the effects of forest cover and landscape heterogeneity may operate at different spatial extents (Holland et al. 2004; Miguet et al. 2016).

Forest cover is highly related to environmental changes occurring in different microhabitats for ants (Ribas et al. 2003; Debuse et al. 2007; De la Mora et al. 2013; Ahuatzin et al. 2019). However, the effects of microclimatic conditions decrease as landscape heterogeneity increases (Tscharntke et al. 2012; De la Mora et al. 2013). At larger spatial extents, landscape heterogeneity seems to be more important in explaining patterns of ant species richness, as we found that the scale of effect was at 900 m. Reynolds et al. (2017) showed that ant species richness in agricultural mosaics of northeastern Swaziland, Africa, responded positively to increases in compositional heterogeneity at spatial extents between 1 and 2 km, suggesting that there is a greater breadth of resources given high environmental variation. Therefore, it is necessary to consider different landscape composition metrics to evaluate the scale of effect, since each metric influences the biological response of organisms in a different way (Atauri and de Lucio 2001; Miguet et al. 2016; Reynolds et al. 2017; San-José et al. 2019). Our results indicate that heterogeneity in the landscape surrounding forest patches is closely related to the variable environments that may either favor the coexistence of different species (by providing a wide variety of resources) or counter it, by altering landscape structural and functional connectivity (Malanson and Cramer 1999; Steckel et al. 2014; San-José et al. 2019).

Studies have shown that multiple factors can influence our ability to evaluate biological responses at different spatial extents (Bellehumeur and Legendre 1998; Holland et al. 2004; Eigenbrod et al. 2011). In fact, the strength of the relationship between any biological response (e.g., richness, species abundance) and an environmental variable often varies according to the spatial scale at which they are measured. Therefore, many of the results in ecological research regarding species or guilds that do not respond to the landscape may be due to problems in study design and failure to select the relevant scale (Eigenbrod et al. 2011; Martin 2018). Moreover, most of the studies that have evaluated the relationship of ants to landscape characteristics at multiple spatial extents have focused on analyzing different biological metrics that include abundance, species richness, and community composition (Spiesman and Cumming 2008; De la Mora et al. 2013; Solar et al. 2016; Egerer et al. 2017). For instance, the scale of effect of landscape structure on ant species richness has been found within spatial extents ranging from 200 to 1000 m, highlighting the effect of landscape context (De la Mora et al. 2013; Solar et al. 2016; Egerer et al. 2017; Reynolds et al. 2017). Specifically, De la Mora et al. (2013) sampled ground and arboreal ants using three different sampling methods (mini-Winkler, destructive sampling, and baits) in an agricultural landscape in Chiapas, Mexico. They found that only leaf litter ants responded to landscape variables at 200 m for forest cover; this is consistent with our results, since we evaluated different sampling methods individually and found that only the ant species richness pattern captured with a Winkler extractor was related to primary forest cover and landscape heterogeneity. Increasing evidence shows that the sampling method can affect the observed results (Rodrigues and Prado 2018); here, we have provided the first evidence of the effect of sampling bias in multiscale ant richness responses to landscape composition.

We conclude that forest cover and landscape heterogeneity influenced ant species richness at a wide range of spatial extents. Based on the evidence that different sampling methods capture distinct trophic guilds with different habitat specificity, the scale of effect for explaining ant species richness depends on the sampling method used. In short, we emphasize the importance of considering that sampling method may influence the ability to assess landscape composition effects on species richness, therefore representing another source of variation in multiscale studies. Finally, it is important to highlight that there may be a cost/benefit analysis to using various trap methods, therefore, applying suitable methods for the target group and research question(s) should dictate which methods are used and what spatial extents are considered.

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