RESEARCH ARTICLE

The surrounding landscape influences the diversity of leaf-litter ants in riparian cloud forest remnants

Miguel Á. García-Martínez¹ *, Jorge E. Valenzuela-González¹, Federico Escobar-Sarria¹, Fabiola López-Barrera¹, Gabriela Castaño-Meneses²

1 Instituto de Ecología, A.C., Xalapa, Veracruz, México, 2 Ecología de Artrópodos en Ambientes Extremos, Unidad Multidisciplinaria de Docencia e Investigación, Facultad de Ciencias, Universidad Nacional Autónoma de México, Campus Juriquilla, Querétaro, México

* magarciamartinez@hotmail.com

Abstract

Riparian vegetation is a distinctive and ecologically important element of landscapes worldwide. However, the relative influence of the surrounding landscape on the conservation of the biodiversity of riparian remnants in human-modified tropical landscapes is poorly understood. We studied the surrounding landscape to evaluate its influence on leaf-litter-ant alpha and beta diversity in riparian remnants in the tropical montane cloud forest region of central Veracruz, Mexico. Sampling was carried out in 12 sites with riparian vegetation during both rainy (2011) and dry (2012) seasons. Ten leaf-litter samples were collected along a 100-m transect per site and processed with Berlese-Tullgren funnels and Winkler sacks. Using remotely-sensed and ground-collected data, we characterized the landscape around each site according to nine land cover types and computed metrics of landscape composition and configuration. We collected a total of 8,684 ant individuals belonging to 53 species, 22 genera, 11 tribes, and 7 subfamilies. Species richness and the diversity of Shannon and Simpson increased significantly in remnants immersed in landscapes with a high percentage of riparian land cover and a low percentage of land covers with areas reforested with Pinus, cattle pastures, and human settlements and infrastructure. The composition of ant assemblages was a function of the percentage of riparian land cover in the landscape. This study found evidence that leaf-litter ants, a highly specialized guild of arthropods, are mainly impacted by landscape composition and the configuration of the focal remnant. Maintaining or improving the surrounding landscape quality of riparian vegetation remnants can stimulate the movement of biodiversity among forest and riparian remnants and foster the provision of ecosystem services by these ecosystems. Effective outcomes may be achieved by considering scientific knowledge during the early stages of riparian policy formulation, in addition to integrating riparian management strategies with broader environmental planning instruments.
Introduction

Riparian remnants are commonly encountered as linear strips of vegetation alongside water-courses and are recognized as important elements of human-dominated landscapes worldwide [1]. These remnants may have distinct species compositions that differ from those of the surrounding habitats [2]. Relative to their extent, they may act as disproportionate reservoirs for local and regional biodiversity [3]. These strips of vegetation are also recognized as important ecological corridors and are used in conservation planning to promote functional landscape connectivity [4]. Moreover, these linear forest remnants provide ecological services (i.e., interception of sediment, litter input, nutrient absorption and regulation of rainwater infiltration) of great value to the functioning of the ecosystem [5].

The conservation value of riparian vegetation remnants in maintaining biodiversity has been widely studied in forest, agricultural, and urban landscapes [6–11]. Most of these studies have focused on comparing diversity and changes in species composition at the habitat scale by assessing different riparian characteristics, such as width [8], structural complexity of vegetation [9,10], or degree of disturbance [3]. Other studies have compared biodiversity associated with riparian remnants with that of adjacent non-riparian habitats [7,12,13].

Furthermore, riparian remnants have been highly modified due to human activities, and they are particularly vulnerable to changes in the surrounding landscape due to their linear configuration (i.e., a high edge to area ratio) [14–16]. Due to this landscape feature, the biodiversity of riparian remnants is expected to be more influenced by the type of matrix (i.e., surrounding non-habitat land uses) [6–8]. Some studies have demonstrated that land uses/cover (LUCs) such as secondary forests, tree crops, or cattle pastures with isolated trees may have disproportionate benefits for the diversity of ants, bats, birds, and frogs associated with riparian remnants in anthropogenic regions [7,12,17,18]. These non-habitat LUCs support riparian biodiversity, acting as complementary and/or supplementary habitats where species can forage and obtain additional resources [19].

However, the relative influence of landscape patterns on riparian biodiversity is poorly understood [1,2]. A few studies have suggested that species diversity and native species abundance are negatively affected when the composition (i.e., covered proportion and number of different land uses) and the configuration (i.e., spatial arrangement of land uses) of the surrounding landscape are human-modified or fragmented, respectively [14–16]. Other studies have indicated that although riparian remnants have been highlighted as biodiversity refuges, these areas may have a reduced capacity to maintain species diversity in highly transformed landscapes [3,12,15]. Therefore, landscape patterns could be an important aspect to consider in management and conservation planning in order to promote functional landscape connectivity [4,8,16].

Useful information for conservation planning has often been based on the diversity of insect groups like ants. In most terrestrial ecosystems, ants are ecologically important and, according to their biological attributes, are very useful for evaluating and monitoring biodiversity and changes in biodiversity [20,21]. In fact, ants represent an excellent model taxon because they respond rapidly to environmental change, represent a variety of trophic levels, are important ecosystem engineers and agents for plant seed dispersal, and have been used effectively as ecological indicators [22,23].

Leaf-litter ants represent more than 50% of the total ant community in forest ecosystems and have high densities and species richness in tropical forest regions [24–26]. They play a major ecological role in these ecosystems as predators, fungus-growers, scavengers, or parasites and are sensitive to environmental changes [27]. At a habitat scale, some studies, carried out in riparian zones, indicate that a higher species diversity is positively related with a high
diversity and structural complexity of the vegetation or environment quality [7,9,13,23]. At a landscape scale, ants can use different land-uses to obtain supplementary and/or complementary resources that may compensate for limited resource availability in natural habitats [28,29]. In fact, leaf-litter ants are influenced by variation in the composition and configuration of their surrounding landscape [30–32]. For this guild of ants, the landscape composition may serve as an indicator of resource availability and environmental conditions, while configuration may serve as an indicator of the movement and dispersal (i.e., matrix permeability) of species within the surrounding landscape [6,30–32]. Thus, richness, abundance, and turnover of species of leaf-litter ant assemblages have been used as tools for establishing conservation priorities or determining the conservation value of endangered ecosystems, including riparian zones [7,9,23,33].

In this study, performed in a tropical montane cloud forest (TMCF) region, we examined the relative influence of the composition and configuration of the surrounding landscape on the conservation value of riparian vegetation remnants, using leaf-litter ant assemblages as a model group. In general, riparian remnants form part of the most threatened tropical ecosystems worldwide [34], and understanding their function as reservoirs of ant diversity, as determined by the surrounding landscape, has important implications for conservation planning. First, we determined alpha (local) and beta diversity (species turnover) of leaf-litter ants in riparian remnants, and then we assessed if the landscape variables, reflecting different levels of anthropogenic change, influenced ant riparian assemblages.

Materials and methods

Ethics statement

Permission to access privately-owned land was given by all land owners. Field collections were carried out under an Ant Collection Permit (SPGA/DGVS/10503/13) issued by the Wildlife Department (Dirección de Vida Silvestre) of Mexico’s Environmental Ministry (SEMARNAT). Due to its focus on invertebrates, this study did not require any approval for animal care and use.

Study area and site selection

The study was conducted in the tropical montane cloud forest region of central Veracruz, Mexico, in the mid-watershed of La Antigua River basin. The climate in the area is mild and humid throughout the year, with total annual precipitation ranging from 1,350 to 2,200 mm and mean annual temperature fluctuating between 12 and 18°C. There are three pronounced seasons: a relatively dry, cool season (October to March), a dry, warm season (April and May), and a wet, warm season (June to September) [34]. In this region, 12 riparian vegetation remnants were selected based on the proportion (range: 5–95%) of forest land cover (i.e., riparian and TMCF land covers) in their surrounding landscape and the accessibility granted by the owners (Fig 1). Patterns of land use and land cover in the watershed and limited access to several zones precluded a balanced design and equidistant sampling. Remnants were located between 1,500 and 2,000 m a.s.l. and separated by a distance ranging from 1 to 18.6 km (Fig 1).

Landscape characterization

We characterized the landscape surrounding each site using a previously generated LUC map of the study region that belongs to an ongoing project (Castillo in prep.). The LUC map was generated from satellite images (SPOT 5; 10 m/pixel) taken on January, 2011. All satellite images were provided by a Mexican satellite receiving station (ERMEX) in 2012. From the
LUC map, we created a 200-m buffer from the center of each site. This buffer size was based on previous studies of the effect of landscape on leaf-litter ants [6,31,35]. In order to verify and update the LUC map, we used the most recent satellite imagery available in Google Earth and ground truthing. When necessary, the area within the buffers was corrected, and changes were digitized on-screen with ArcGIS 10.2®. The land-use classes in the studied landscape were standardized considering previous studies on the TMCF landscape of this region [34,36,37]. Nine LUC types were defined (Table 1). We used the Patch Analyst extension for ArcMap [38] to compute the spatial metrics of the composition and configuration of the landscape within each buffer of 200 m surrounding the study remnants (S1 Table).

We considered riparian remnants to be linear strips of vegetation immediately adjacent to rivers and streams, which widely varied in width and level of impact due to anthropogenic activities [1]. For the landscape composition metrics, we estimated the percentage of land covers with tropical montane cloud forest (TMCF), riparian vegetation, scrub fallow, areas

Fig 1. Location of the study sites in central Veracruz, Mexico. The red circles represent 200-m-buffers around each remnant of riparian vegetation where leaf-litter ants were sampled. Blue lines are the tributaries of the Antigua River watershed. In the inset are indicated the location, in Mexico, of the study area (red square), the state of Veracruz (black polygon), and the location of Mexico (white polygon) between North and Central America. This map was generated by the first author (MAGM) using ArcGIS 10.2® and vector data models available in the GIS website of the Mexican commission for the knowledge and use of biodiversity (CONABIO, http://www.conabio.gob.mx/informacion/gis/) under a CC BY license.

doi:10.1371/journal.pone.0172464.g001
reforested with *Pinus*, tree crops, shrub crops, cattle pasture with isolated trees, cattle pasture, and human settlements and infrastructure within the surrounding landscape (Table 1). In the studied region, some LUCs mimic TMCF cover (e.g., riparian vegetation, scrub fallow, areas reforested with *Pinus*, tree crops), and, when these were contiguous, their edges were not always evident in the observed satellite images. For this reason and in order to verify the interacting LUCs within the 200-m-radius buffers, we did ground truthing to define the natural boundaries among LUCs based on the composition and abundance of plant species (Table 1).

Landscape configuration metrics included the shape and width of each of the 12 focal riparian remnants of this study. The remnant shape was estimated with the shape index proposed by Patton [39]:

\[ SI = \frac{P}{2 \cdot \sqrt{\pi \cdot A}} \]  

where \( P \) and \( A \) are the patch perimeter and area, respectively. The higher the \( SI \) values, the higher the shape complexity (perfect circle, \( SI = 1.0 \)). The remnant width was the mean of 10

| Land cover type                          | Description                                                                                                                                                                                                                                                                                                                                 |
|-----------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Tropical montane cloud forest (TMCF)   | Forest fragments with different degrees of disturbance, including secondary forests. Canopy height usually varied between 15 and 30 m and average diameter at breast height (DBH) is greater than 15 cm. The most common species are *Liquidambar styraciflua* L., *Miconia glaberrima* Naudin, *M. mexicana* Naudin, *Pilocourea padifolia* (Roem. & Schult.), *Quercus germana* Schltdl. & Cham., *Q. insignis* M.Martens & Galeotti, *Q. laurina* Liebm. *Q. leiophylla* A.DC., *Q. salicifolia* Née, *Q. xalapensis* Bonpl., *Turpinia insignis* Tul. |
| Riparian vegetation                     | Strips of vegetation immediately adjacent to rivers and streams. Canopy height usually varied between 10 and 25 m and average tree DBH is between 15 and 80 cm. The most common species are *Arachnothryx capitellata* Hemsl., *Buddleja cordata* Kunth, *Meliosma alba* Walp., *Saurauia pedunculata* Hook., *Platanus mexicana* Moric., *Trema micranthum* (L.), *Turpinia occidentalis* G.Don. |
| Scrub fallow                            | Second-growth vegetation dominated by shrubs, herbs, and climbing plants. The most common species are *Cestrum nocturnum* L., *Cyphomandra betacea* (Cav.), *Citrus* spp., *Perrottetia longistyli* Rose, *Piper* spp., *Pteridium aquilinum* (L.), *Rubus* spp., *Smallanthus maculatus* (Cav.) and *Tithonia diversifolia* A.Gray. |
| Areas reforested with *Pinus*           | Different forested areas planted with a single *Pinus* species with a maximum DBH of 12 cm. Management practices include understory clearing and selective logging. Planted species varies widely depending on the provided saplings to farmers by SEMARNAT. At the moment of this study, the most common species were *Pinus leiophylla* Schltdl. & Cham., *P. maximinoi* H.E.Moore, *P. michoacana* Martinez, *P. patula* Schltdl. & Cham., and *P. pseudostrobus* Lindl. |
| Tree crops                              | Agroforestry systems, including coffee plantations shaded by TMCF species or exotic tree species mainly *Inga* spp.                                                                                                                                                                                                                              |
| Shrub crops                             | Row crops, mainly, of maize, beans, berries, or potato.                                                                                                                                                                                                                                                                                       |
| Cattle pasture with isolated trees      | Active pastures with isolated trees and shrubs. The most common species are *Acacia* spp., *Cedrela odorata* L., *Lippia myriocephala* Schltdl. & Cham. *Psidium guajava* L., and *Randia* spp.                                                                                                                                                  |
| Cattle pasture                          | Active and intensive pastures usually covered by exotic grasses species like *Andropogon* spp., *Panicum maximum* Jacq., and *Paspalum* spp.                                                                                                                                                                                                      |
| Human settlements and infrastructure    | Human populations, cities, or localities, including roads and highways.                                                                                                                                                                                                                                                                     |

Table 1. Land cover types determined from field verification and remotely-sensed data in the studied landscapes of Central Veracruz, Mexico.

doi:10.1371/journal.pone.0172464.t001
perpendicular distances, recorded at 10-m intervals along a 100-m transect, between the stream edge and that of the adjoining LUC.

Ant sampling

Sampling was carried out along a 100-m-long transect in each remnant. Ten 1-m² quadrats of leaf-litter were collected at 10 m intervals along the transect. Five samples were processed in Berlese-Tullgren funnels with a 25-watt light bulb for 72 h, and the other five samples were processed in Winkler sacks for 72 h [40]. These distinct techniques were alternated along the length of each transect. Collections were repeated in both the 2011-rainy and 2012-dry seasons, such that each site had 20 litter samples, 10 in the wet season and 10 in the dry season. All collected ants were preserved in 70% ethanol, and one to five of the collected specimens per sample that differed morphologically were dry-mounted. Only worker ants were counted in the samples and recorded as incidence data for analysis. The Mackay and Mackay [41] key was used to identify ant genera, along with several additional keys for species identification, depending on the genus involved [42–45]. The specimens that could not be identified with the respective keys were identified to morphospecies. All ants, including representative vouchers of each morphospecies, were deposited in the Entomological Collection of the Instituto de Ecología A.C. in Xalapa, Veracruz, Mexico (IEXA; Reg. SEMARNAT: Ver. IN.048.0198).

Alpha and beta diversity

Number of occurrences of a species at a site, across both wet and dry season sampling, was used as a measure of abundance (with maximum abundance = 20). We calculated the inventory reliability for each remnant using the coverage estimator, which is a less biased estimator of sample completeness than non-parametric methods [46]:

$$\hat{C}_n = \left( 1 - \frac{f_1}{n} \left[ \frac{n - 1}{n - 1} \frac{f_1}{f_1 + 2f_2} \right] \right) * 100$$

where \(n\) is the number of occurrences summed across all species of a given site, and \(f_1\) and \(f_2\) are singletons (species each represented by only a single occurrence) and doubletons (species each represented by exactly two occurrences), respectively. This sample completeness (\(\hat{C}_n\)) indicates the proportion of the 'total community' represented by the trapped species [46] and enables comparison of the diversity of assemblages at the same sample coverage [46,47]. When \(\hat{C}_n \approx 100\%), sampling is complete given the effort and capture technique used [46]. Values of \(\hat{C}_n\) were calculated using iNEXT package for R [48].

Ant diversity was evaluated using Hill numbers [49], following Jost’s [50] proposal. These measures are recommended for comparative studies of diversity because they meet the replication principle [51] and are easy to interpret [47]. We used Hill numbers of order 0 (\(\hat{D}_0\), species richness), 1 (\(\hat{D}_1\), exponential of Shannon’s entropy), and 2 (\(\hat{D}_2\), inverse Simpson concentration). Species richness (\(\hat{D}_0\)) is not sensitive to species abundances and thus gives disproportionate weight to rare species [50]. Shannon diversity (\(\hat{D}_1\)) weighs each species according to its abundance in the community; hence, it can be interpreted as the number of ‘common’ or ‘typical’ species in the community [50]. Finally, Simpson diversity (\(\hat{D}_2\)) can be interpreted as the number of ‘very abundant’ or ‘dominant’ species in the community [50]. To compare each diversity measure among remnants, we used 95% confidence intervals in which significant differences were indicated by non-overlapping confidence intervals [52].

To evaluate differences in species’ dominance, rarity, and community evenness among study remnants and thus better interpret our results, ant abundance was represented by rank-
abundance species curves or Whittaker plots [53]. We plotted the proportional abundance of each species, ordered from the most to the least abundant, in order to show differences in species’ dominance and rarity in addition to the assemblage evenness among remnants.

For analyzing beta diversity, we determined the compositional similarity among assemblages using the indices of Jaccard, Sørensen, and Morisita-Horn. These indices have values ranging from 0 (minimal similarity) to 100 (maximum similarity) [53]. We used these indices because, as with the Hill numbers, each provides distinct information about compositional similarity depending on their sensitivity to species’ abundances (i.e., sensitivity to rare or common species) [50]. The Jaccard index only takes into account shared species and presence/absence of species between sites [50]. The Sørensen index relates the sum of the lower of the two abundances for shared species with the total abundance observed between sites [53]. The Morisita-Horn index relates the abundance of each species with the abundance of the most abundant species between sites [53]. In a unified framework of analysis under a scheme of diversity measured as the effective number of species, the Jaccard, Sørensen, and Morisita-Horn indices represent simple monotonic transformations of the beta diversity of orders 0 ($0D_β$), 1 ($1D_β$), and 2 ($2D_β$), respectively. In other words, the beta diversity of orders 0 ($0D_β$), 1 ($1D_β$), and 2 ($2D_β$) are inversely related to the Jaccard, Sørensen, and Morisita-Horn indices of compositional similarity, respectively (i.e., if the communities have a high compositional similarity, then the set of communities must have a low beta diversity) [50].

The compositional similarity among remnants was represented by a cluster analysis using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) linkage technique. For post hoc analyses, similarity profile tests (SIMPROF) were used as statistical tests to compare similarity among assemblages in the PRIMER program version 6.1.16 [54]. SIMPROF test assumes that a real clustering of assemblages will be evidenced by an excess of smaller and/or larger similarities than expected under the null hypothesis that all assemblages are drawn from the same species assemblage [55].

**Landscape predictors**

In order to identify the dominant landscape predictors influencing alpha and beta ant diversity of riparian remnants, we followed both univariate and multivariate selection procedures for regression-based models. As these statistical techniques are sensitive to collinearity between predictor variables, we used the Spearman correlation coefficient to exclude correlated variables. For each set of significantly correlated variables we retained only one that was considered to be the most intuitive and interpretable.

We used generalized linear models (GLM) to assess the independent effects of each landscape predictor on each metric of alpha diversity (i.e., a single univariate regression between a response and a predictor variable). We applied a Gaussian error distribution for continuous variables (i.e., species richness, Shannon and Simpson diversity) after testing for normality (Shapiro–Wilk test). Abundance (a count-dependent variable) was assessed assuming a Poisson error distribution. For each multiple regression model (i.e., a multiple univariate regression between a response and several predictor variables), we used the variance inflation factors (VIF) to exclude landscape predictors that would affect the accuracy of the estimates, using the car package for R version 3.2.2. We followed an information-theoretic approach and multimodel inference to assess the relative effect of each landscape predictor on each metric of alpha diversity using the package gmult for R version 3.2.2 [56,57]. This function built a set of models representing all possible combinations of landscape predictors for each diversity measure. It also computed the Akaike’s information criterion, corrected for small samples (AICc) for each built model. To correct for the overdispersion associated with count data, abundance
was assessed with qAICc instead of AICc values \[57\]. The goodness-of-fit of the models was estimated as the explained deviance for each complete model using the \textit{modEvA} package for R version 3.2.2 \[58\].

We used distance-based linear models (DistLM) for analyzing and modelling the relationships between the distance/similarity matrices of ant assemblages and the landscape predictors. Using a multiple regression model, this routine performed a partition according to the variation in the data cloud that was described by the resemblance matrices. Then, it performed a permutational test for the multivariate null hypothesis that no relationship existed between explanatory and response matrices, based on a chosen resemblance measure and using permutations of the samples to obtain a P-value. Finally, it modeled the percentage of overall variation in the compositional similarity of ant assemblages accounted for by each landscape predictor \[59\]. In this procedure we considered the compositional similarity between assemblages as response matrices, using the Jaccard ($\bar{D}_{\beta}$), Sørensen ($\bar{D}_{\beta}$), and Morisita-Horn ($\bar{D}_{\beta}$) indices. The Akaike’s Information Criterion for small samples (AICc) was tested in the analysis to provide a comprehensive evaluation of appropriate predictors to include in the models. The selection procedure of the models was “BEST”, which examines the value of the selection criterion for all possible combinations of predictor variables. These analyses were carried out using PRIMER ver. 6.1.18 and PERMANOVA+ ver. 1.0.8 \[59,60\].

Following Burnham and Anderson \[56\], we considered a set of models with equivalently strong empirical support and similar plausibility, or when the difference in the qAICc or AICc values were less than 2 in comparison to the best model (i.e., the one with lowest qAICc or AICc value). To evaluate the importance of each predictor and to produce model-averaged parameter estimates, we used Akaike weights ($w_i$), which represent the probability that a particular model would be selected as the best fitting model if the data were to be collected again under identical conditions. This model can therefore be considered as the best model for a particular dataset. Thus, we summed $w_i$ of ranked models until the total was $> 0.95$. The set of models for which a sum of $w_i$ was 0.95 represented a set that had a 95%-probability of containing the true best model. The relative importance of each predictor was assessed based on the sum of Akaike weights ($\Sigma w_i$) of each candidate model in which the predictor appeared. We considered a given landscape predictor to be an important explanatory variable for a given diversity measure when it showed a high sum of Akaike weights (i.e., considering each candidate model in which it appeared) and when its model-averaged unconditional variance was lower than the model-averaged parameter estimate \[56\].

In order to examine whether the proximity in remnants or buffers of surrounding landscape (Fig 1) influenced the GLM or DistLM regressions, we tested for spatial autocorrelation in the landscape predictors \[61\]. We examined the degree of spatial autocorrelation in the residuals of the GLM regressions with the Moran’s test for spatial autocorrelation using a spatial weights matrix in the \textit{spdep} package for R version 3.2.2 \[62\]. For the calculation of Moran’s I, we used nearest neighbor distances as the metric and the permutation test option. For examining the spatial autocorrelation in the residuals of the DistLM multivariate regressions, we performed a multivariate spatial Mantel analysis using the \textit{MRM} function in the \textit{ecodist} package for R version 3.2.2 \[63,64\]. None of the variables examined for the GLM or DistLM regressions displayed significant spatial autocorrelation at any distance (S2 Table).

Results

Landscape patterns

In the studied landscapes, riparian land cover varied from 6% (R2) to 66% (R9), and it was negatively correlated with the land covers with areas reforested with \textit{Pinus} ($\rho = -0.71$, \[57\].
P < 0.05), cattle pastures (ρ = -0.88, P < 0.05), and human settlements and infrastructure (ρ = -0.74, P < 0.05, S1 Table). TMCF land cover varied from 7% (R1) to 45% (R12), cattle pastures with isolated trees from 0% (R9) to 28% (R4), and scrub fallow from 0% (R1, R10, R11, and R12) to 28% (R6). The highest proportion of tree crop land cover was observed in R8 (10%), followed by R3 (1%), R4, and R5 (less than 1% each), and the remaining had 0%. The highest shrub crop land cover was found in R3 and R4 (4% each), followed by R2 and R7 (2%), R6 (1%), R5, and R10 (less than 1% each), and the remaining had 0%. The percentage of land covers with TMCF, scrub fallow, tree crops, shrub crops, and cattle pasture with isolated trees within the surrounding landscape were not significantly correlated among them or to any other land cover (P > 0.05).

**Alpha and beta diversities**

We collected 8,684 individuals belonging to 53 species, 22 genera, 11 tribes, and 7 subfamilies (S3 Table). Subfamily Myrmicinae had the highest number of tribes, genera, and species. The richest genus was *Stenamma* (7 spp.), followed by *Adelomyrmex* (5 spp.), *Hypoponera*, *Nyländeria*, and *Pheidole* (5 spp. each), *Solenopsis* and *Strumigenys* (3 spp. each), and *Brachymyrmex*, *Eurhopalothrix*, *Gnamptogenys*, *Labidus*, and *Temnothorax* (2 spp. each). The 10 remaining genera were represented by only one species.

The average sample coverage was 97% (range: 92–98%). The overall sample coverage, considering the 12 riparian remnants, was 99% (S4 Table). Abundance varied between 83 (R11) and 118 (R3) species occurrences, and the assemblage structure changed across the sampled remnants (S1 Fig). The general pattern observed indicated a decrease in species dominance from R1 to R12, and the dominant species were different in each remnant. Species richness \((\alpha D)\) varied significantly from 9 (R1 and R2) to 26 (R12) species. The diversity of Shannon (\(1D\)) increased significantly from R2 (8 spp.) to R12 (23 spp.), and that of the order 2 (\(2D\)) increased significantly from R4 (7 spp.) to R11 and R12 (19 spp.) (S4 Table).

The compositional similarity using cluster analysis and SIMPROF tests indicated that the Jaccard index significantly separated three assemblage clusters with similarities of 34% (\(\pi = 3.27, P = 0.006\), S2 Fig). The Sørensen index significantly separated two assemblage clusters at a similarity of 33% (\(\pi = 4.5, P = 0.001\), S2 Fig). Meanwhile, the Morisita-Horn index significantly separated six assemblage clusters at similarities of 42% (\(\pi = 3.7, P = 0.001\)), 53% (\(\pi = 3.19, P = 0.01\)), 66% (\(\pi = 6.27, P = 0.001\)), 70% (\(\pi = 5.87, P = 0.01\)), and 73% (\(\pi = 8.92, P = 0.007\), S2 Fig).

**Landscape predictors of alpha and beta diversity**

Riparian land cover in the landscape was one of the most important predictors that explained abundance, richness, and diversity of species. TMCF land cover was only significantly related with ant abundance. Meanwhile, land covers with cattle pastures with isolated trees, scrub fallow, shrub crops, and tree crops were not significantly related with any abundance or diversity variable. The multiple models explained between 65 and 88% of the deviance (Fig 2).

GLM analyses indicated that abundance was negatively (and independently) explained by the riparian and TMCF land covers in the landscape as well as by the shape and width of the focal riparian remnant (Table 2). The information-theoretic approach and multi-model inference analysis indicated that in a multiple model, riparian land cover and shape of the focal remnants were the most important predictors of abundance (Fig 2a). Species richness was positively (and independently) explained by riparian land cover and the shape and width of the focal riparian remnants (Table 2). In a multiple model, riparian land cover and shape of the focal remnant were the most important predictors of species richness (Fig 2b). Shannon
diversity was positively (and independently) explained by riparian land cover and width of the focal riparian remnants (Table 2). In a multiple model, riparian land cover and shape of the focal remnant were equally important predictors of Shannon diversity (Fig 2c). Simpson diversity was positively (and independently) explained by riparian land cover and the width of the focal riparian remnant (Table 2). In a multiple model, riparian land cover and shape of the focal remnants were equally important predictors of Shannon diversity (Fig 2d).

The distance-based linear modelling (DistLM) indicated that species composition (Jaccard index, $J_p$) was independently explained by the riparian and TMCF land covers in the landscape as well as by the shape and width of the focal riparian remnant (Table 2). The information-theoretic approach and multi-model inference analysis indicated that in a multiple model, the riparian land cover within the landscape and the width of the focal riparian remnant were the most important predictors of Jaccard similarity (Fig 3a). Compositional similarity of order 1 ($\beta_1$, Sørensen index) was independently explained by the riparian land cover in the landscape and the shape and width of the focal riparian remnant (Table 2). In a multiple model, the width of the focal riparian remnants was the most important predictor of Sørensen similarity (Fig 3b). Compositional similarity of order 2 ($\beta_2$, Morisita-Horn index) was independently explained by the riparian land cover in the landscape and by the shape and width of the focal riparian remnants (Table 2). In a multiple model, the riparian land cover within the landscape and the width of the focal riparian remnant were the most important predictors of Morisita-Horn similarity (Fig 3c).
Table 2. Effects of the landscape characteristics on alpha and beta diversity of leaf-litter ants associated with remnants of riparian vegetation.

Relationships between landscape predictors and alpha diversity metrics and between landscape predictors and beta diversity metrics are indicated separately.

| Model Type                                      | Metric                  | Predictor               | Z or t Statistic | d.f. | P       | AICc   |
|------------------------------------------------|-------------------------|-------------------------|------------------|------|---------|--------|
| A) Single and univariate generalized linear models | Abundance               | Riparian land cover     | -3.63            | 10   | 0.0002  | 188.39 |
|                                                 | Abundance               | TMCF land cover         | -2.4             | 10   | 0.0100  | 205.26 |
|                                                 | Abundance               | Shape of focal remnant  | -3.41            | 10   | 0.0006  | 192.45 |
|                                                 | Abundance               | Width of focal remnant  | -3.07            | 10   | 0.0020  | 196.91 |
|                                                 | Species richness        | Riparian land cover     | 4.82             | 10   | 0.0006  | 71.01  |
|                                                 | Species richness        | TMCF land cover         | 1.54             | 10   | 0.1500  | 81.77  |
|                                                 | Species richness        | Shape of focal remnant  | 3.87             | 10   | 0.0030  | 74.42  |
|                                                 | Species richness        | Width of focal remnant  | 3.85             | 10   | 0.0030  | 74.52  |
|                                                 | Shannon diversity       | Riparian land cover     | 8.33             | 10   | <0.0001 | 57.99  |
|                                                 | Shannon diversity       | TMCF land cover         | 1.82             | 10   | 0.0986  | 76.42  |
|                                                 | Shannon diversity       | Shape of focal remnant  | 2.20             | 10   | 0.0523  | 75.11  |
|                                                 | Shannon diversity       | Width of focal remnant  | 6.30             | 10   | <0.0001 | 63.59  |
|                                                 | Simpson diversity       | Riparian land cover     | 8.54             | 10   | <0.0001 | 53.76  |
|                                                 | Simpson diversity       | TMCF land cover         | 1.80             | 10   | 0.1020  | 72.80  |
|                                                 | Simpson diversity       | Shape of focal remnant  | 1.88             | 10   | 0.0889  | 72.52  |
|                                                 | Simpson diversity       | Width of focal remnant  | 6.70             | 10   | <0.0001 | 58.73  |
| B) Multiple and univariate generalized linear models | Abundance               | Riparian land cover     | -2.50            | 10   | 0.0125  | 188.39 |
|                                                 | + Shape of focal remnant|                        | -2.01            | 9    | 0.0449  | 183.86 |
|                                                 | Species richness        | Riparian land cover     | 5.50             | 10   | 0.0004  | 71.01  |
|                                                 | + Shape of focal remnant|                        | 4.53             | 9    | 0.0014  | 61.46  |
|                                                 | Shannon diversity       | Riparian land cover     | 4.62             | 10   | 0.0013  | 57.99  |
|                                                 | + Width of focal remnant|                        | 3.16             | 9    | 0.0115  | 53.73  |
|                                                 | Simpson diversity       | Riparian land cover     | 5.072            | 10   | 0.0007  | 53.76  |
|                                                 | + Width of focal remnant|                        | 3.734            | 9    | 0.0047  | 47.24  |
| C) Single and multivariate distance-based linear models | Jaccard similarity    | Riparian land cover     | 3.55             | 1    | 0.0027  | 91.06  |
|                                                 |                        | TMCF land cover         | 2.23             | 1    | 0.0369  | 92.29  |
|                                                 |                        | Shape of focal remnant  | 2.75             | 1    | 0.0120  | 91.79  |
|                                                 |                        | Width of focal remnant  | 3.54             | 1    | 0.0032  | 91.07  |
|                                                 | Sørensen similarity     | Riparian land cover     | 6.03             | 1    | 0.0008  | 87.92  |
|                                                 |                        | TMCF land cover         | 2.20             | 1    | 0.0718  | 91.20  |
|                                                 | Sørensen similarity     | Shape of focal remnant  | 3.03             | 1    | 0.0283  | 90.41  |
|                                                 | Sørensen similarity     | Width of focal remnant  | 6.18             | 1    | 0.0011  | 87.81  |
|                                                 | Morisita-Horn similarity| Riparian land cover     | 7.47             | 1    | 0.0018  | 83.04  |
|                                                 | Morisita-Horn similarity| TMCF land cover         | 2.56             | 1    | 0.0821  | 87.00  |
|                                                 | Morisita-Horn similarity| Shape of focal remnant  | 4.01             | 1    | 0.0243  | 85.69  |
|                                                 | Morisita-Horn similarity| Width of focal remnant  | 10.26            | 1    | 0.0003  | 81.26  |
| D) Multiple and multivariate distance-based linear models | Jaccard similarity    | Riparian land cover     | 9.97             | 1    | 0.0004  | 91.06  |
|                                                 | + Width of focal remnant|                        | 3.91             | 1    | 0.0003  | 92.83  |

(Continued)
Discussion

This study supports the importance of variables at the landscape level and their effect on the alpha and beta diversity of leaf-litter ants associated with riparian vegetation remnants in the TMCF region of central Veracruz, Mexico. Our results also improve the understanding of the main drivers determining the riparian assemblages of leaf-litter ants in fragmented tropical montane landscapes. Overall, in the studied landscape alpha diversity metrics and compositional similarity were mainly shaped by the extent of riparian land cover and the width of riparian remnants.

In general, species richness, Shannon and Simpson diversity increased significantly in remnants within landscapes with a high percentage of riparian land cover and a low percentage of land covers with areas reforested with *Pinus*, cattle pastures, and human settlements and infrastructure (S1 and S4 Tables, Fig 2). These results are consistent with other studies that also found that ant diversity is positively related to the amount of remaining natural habitat in the landscape [6,8,30,31]. This is not surprising, as this ecological group is expected to be vulnerable to changes in the amount of available habitat [32]. With an increase in riparian land cover, we could expect a greater potential availability and quality of nesting sites, in addition to a larger supply of food, as well as favorable environmental conditions that would support richer leaf-litter ant assemblages [3,8–10,32,65].

The observed diversity pattern may additionally be related to the heterogeneity of the studied landscape, where several small riparian remnants were more isolated from each other in comparison to a few large and less isolated remnants (S1 Table). Although our results indicate that riparian land cover in the surrounding landscape is the main driver of species diversity, the shape and width of focal riparian remnants were also important predictors (Fig 2). We found that the width of focal riparian remnants was an important predictor positively (and significantly) related to increases in Shannon and Simpson diversity. Meanwhile, the shape of remnants was significantly related to increases in species richness and decreases in abundance of leaf-litter assemblages. Commonly, a high edge to area ratio increases species loss, and Didham [19] suggests that this effect is likely to be particularly severe for remnants of riparian vegetation. Surprisingly, we found contradictory results for leaf-litter ants. Even so, shape complexity is, until now, a landscape attribute that has not been well studied [19,66]. Patch shape complexity has been highlighted as influential in the extent to which edge effects permeate habitat patches and reduce core area for patch specialists [66]. In this study, the significance of riparian remnants with an irregular shape may be that they counterbalance the loss of species diversity due to spillover or the active movement of leaf-litter ant species from the surrounding land covers [67]. In this sense, riparian remnants could act as supplementary or complementary habitats and offer various resources to a species pool of leaf-litter ants that

| Table 2. (Continued) |      |      |      |      |
|----------------------|------|------|------|------|
| + Shape of focal remnant | 2.36 | 1    | 0.0207 | 95.09 |
| Sørensen similarity + |      |      |      |      |
| Riparian land cover   | 6.02 | 1    | 0.0008 | 87.92 |
| + Width of focal remnant | 6.17 | 1    | 0.0004 | 89.39 |
| + Shape of focal remnant | 3.03 | 1    | 0.0291 | 91.89 |
| Morisita-Horn similarity + |      |      |      |      |
| Riparian land cover   | 7.46 | 1    | 0.0023 | 83.04 |
| + Width of focal remnant | 10.26 | 1  | 0.0005 | 83.71 |
| + Shape of focal remnant | 4.01 | 1    | 0.0252 | 86.22 |

doi:10.1371/journal.pone.0172464.t002
Fig 3. Landscape predictors included in the 95% confidence set of the models (gray bars) and in the ΔAICc < 2 set of the models (black bars) for explaining the compositional similarity indicated by Jaccard, Sørensen, and Morisita-Horn indices of leaf-litter ant assemblages associated with remnants of riparian vegetation in central Veracruz, Mexico. The importance of each predictor is shown by the sum of Akaike weights (∑ w_i, panels in the left side). Panels on the right side indicate the values of the averaged model parameter estimates (β) ± unconditional variance of information-theory-based model selection and multi-model inference. The sign (±) of parameter estimates represents a positive or negative
cannot distinguish between habitat and matrix [19]. The species that move to riparian remnants or use them in some way may differ depending on the surrounding landscape composition [67]. For example, in landscapes with remnants that are wider and more complex in shape, we collected cryptic and specialist species reported for TMCF (e.g., *Adelomyrmex* spp., *Eurhopalothrix* spp., *Stenamma* spp., and *Strumigenys* spp.; S3 Table) [24]. In contrast, in landscapes composed of narrow and less complex riparian remnants, we found generalist species that are common in open areas and tolerant to these conditions (e.g. *Brachymyrmex* spp., *Nylanderia* spp., and *Solenopsis* spp.; S3 Table) [13].

In the comparison of compositional similarity, we found from 2 (Sørensen index) to 6 (Morisita-Horn index) significant clusterings or effective communities sensu Jost [50] of leaf-litter ant assemblages (S2 Fig). These results indicate that ant assemblages become more different when abundant species are considered in the similarity composition. This pattern of differentiation in composition may be explained by the relatively high fraction of unique remnant species (34% of the total collected species) and low fraction of numerically dominant species (7%, S1 Table, S1 and S2 Figs). This result has been previously shown for leaf-litter ant assemblages associated with TMCF fragments and cattle pastures with isolated trees in the studied region [3,13,24]. Therefore, this high species turnover among remnants suggests that the maintenance of even highly disturbed riparian remnants may play a strategic role in the conservation of myrmecofauna and probably of other organisms in the severely transformed landscape of this region.

The observed compositional similarity of ant assemblages is likely a function of the percentage of riparian land cover in the surrounding landscape (Table 2, Fig 3). Some studies have suggested that there is a general pattern of differentiation in the compositional similarity that corresponds with changes in the configuration and composition of the surrounding landscape [32]. In particular, our results are consistent with previous studies suggesting that shifts in species composition are attributable to variations in the proportion of available habitat and the land cover types present in the surrounding landscape, mainly when there are large extensions of open areas like cattle pastures [68,69]. We observed in the studied landscape that certain surrounding land uses, such as pine plantations and human settlements or infrastructure, are the main threats to riparian land cover (S1 Table). That kind of surrounding landscape was also reported as an important driver of compositional similarity for ants in a sandhill habitat in Florida, USA [30]. In our study, these land uses led to a replacement of specialist ant species by generalists within riparian remnants. Additionally, that surrounding landscape plays an important role in structuring ant assemblages via influencing the dynamic of colonization-extinction and limiting the dispersal of communities across the fragmented region [30]. Thus, at the landscape scale, the composition of the surrounding landscape may explain the variation in compositional similarity among riparian assemblages (S1 Table, Fig 3).

In conclusion, this study found evidence that the diversity of leaf-litter ants, a highly specialized guild of arthropods, is significantly impacted by both composition and configuration of the surrounding landscape. At the small landscape-scale (200-m-buffers), considering nine land cover types in a highly transformed landscape, the extent of the riparian land cover within the surrounding landscape determined the capacity of riparian remnants to conserve ants. Based on our results and the bioindicator capacity of leaf-litter ant assemblages, maintaining...
the remaining riparian remnants could be a viable strategy to conserve biodiversity and environmental services in the study region (Fig 1). Conservation actions should involve the active protection and restoration of native forest (TMCF and riparian vegetation) in order to increase the permeability of the surrounding landscape at small scales. That strategy may result in a positive impact on biodiversity conservation. Viable alternatives to reconcile conservation and land productivity should be explored (forest-pastoral systems, expansion of riparian vegetation with useful native tree plantations, enrichment of pine plantations, etc.) [70,71].

Many studies have investigated the optimal strategies in riparian zones for conserving a wide range of taxa, including amphibians, reptiles, birds, mammals, and plants [11,14–16,72]. However, data on invertebrates are still limited [6,8]. The observed results for the studied bioindicator group suggest that policies and strategies that take into account habitat-level features in order to improve the conservation value of riparian remnants should also consider features of the surrounding landscape. In particular, riparian remnants are highly influenced by their surroundings, and increasing forested areas in the surrounding landscape, as well as the width and heterogeneous shape of riparian remnants, will stimulate biodiversity movement. In addition, such a strategy could foster and protect the ecosystem services offered by the forest and riparian vegetation in the studied landscape [34]. Finally, effective outcomes will only be achieved if scientific knowledge is considered during the early planning stages of policies that affect riparian zones, in addition to the subsequent integration of riparian policies into broader environmental planning instruments [8].

Supporting information

S1 Fig. Rank-abundance curves of the leaf-litter ant assemblages associated with remnants of riparian vegetation in central Veracruz, Mexico. Only species with a relative abundance higher than 5% (above dashed line) in a given remnant are shown. Ant species are numbered in accordance with S2 Table.
(TIF)

S2 Fig. Dendrograms from standard hierarchical clustering based on the Jaccard ($D_β$, $S_β$) and Morisita-Horn ($D_β$) similarity indices of the leaf-litter ant assemblages associated with remnants of riparian vegetation. The dendrogram displays with black continuous lines the divisions for which the SIMPROF test rejects the null hypothesis (where assemblages in that group have no further structure to explore) and with red dashed lines the groups of assemblages not separated (at $P < 0.05$) by SIMPROF.
(TIF)

S1 Table. Landscape metrics for all twelve remnants of riparian vegetation in central Veracruz, Mexico.
(XLSX)

S2 Table. Results from spatial autocorrelation of the landscape predictors to examine whether the proximity in remnants or buffers of surrounding landscape influenced the regressions of generalized linear models (A and B) or multivariate distance-based linear models (C and D).
(XLSX)

S3 Table. Leaf-litter ants collected in each remnant of riparian vegetation in the central mountainous region of Veracruz, Mexico. All species are sorted by subfamily and tribe. Number listed indicate the observed species occurrences in each site.
(XLSX)
S4 Table. Sampling completeness and alpha diversity of the leaf-litter ants associated with 12 remnants of riparian vegetation in central Veracruz, Mexico. The lower and upper 95% confidence intervals for each diversity measure are given in brackets. Numbers listed as abundance indicate the sum of all species occurrences per remnant during both dry and wet seasons.

Acknowledgments

We are grateful for Dora Luz Martinez Tlapa, Gibran Renoy Perez Toledo and Luis N. Quiroz-Robledo for their assistance in the processing of samples and ant identification. For Javier Tolome Romero, Victor Vazquez-Reyes, and Claudia Gallardo Hernandez for technical assistance in the field. For Rosario Landgrave Ramirez for technical assistance in GIS, and to Gonzalo Castillo Campos for advising us in the LUC classification. For Delfino Hernandez Lagunes for technical assistance in the Entomological Collection IEXA-INECOL. For Ehdiblando Presa-Parra for his help in references management. For John Longino and Michael Branstetter for reviewing our identifications of Adelomyrmex and Stenamma specimens. English version of the manuscript was reviewed by Allison Marie Jermain. Miguel Angel Garcia Martinez acknowledges the scholarship and financial support provided by the Consejo Nacional de Ciencia y Tecnologia (CONACyT 250343/373712/347058, Convocatoria 290733) and the Doctoral Program of the Instituto de Ecologia A.C. (INECOL). Funding was provided by INECOL (project 902-11-10204) and CONACyT (project CB 2008-101542-F).

Author Contributions

Conceptualization: MAGM FLB GCM FES JEVG.

Formal analysis: MAGM.

Funding acquisition: FES JEVG.

Investigation: MAGM FLB GCM FES JEVG.

Methodology: MAGM FLB FES.

Project administration: FES JEVG.

Resources: MAGM FES JEVG.

Software: MAGM.

Supervision: MAGM FLB GCM FES JEVG.

Validation: MAGM FLB GCM FES JEVG.

Visualization: MAGM FLB GCM FES JEVG.

Writing – original draft: MAGM.

Writing – review & editing: MAGM FLB GCM FES JEVG.

References

1. Naiman RJ, Decamps H, Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological applications 3: 209–212. doi: 10.2307/1941822 PMID: 27759328

2. Granados-Sánchez D, Hernández-García M, López-Ríos G (2006) Ecología de las zonas ribereñas. Revista Chapingo Serie ciencias forestales y del ambiente 12: 55–69.
3. Garcia-Martinez MÁ, Escobar-Sarria F, López-Barrera F, Castaño-Meneses G, Valenzuela-González JE (2015) Value of Riparian Vegetation Remnants for Leaf-Litter Ants (Hymenoptera: Formicidae) in a Human-Dominated Landscape in Central Veracruz, Mexico. Environmental entomology 44: 1488–1497. doi: 10.1093/ee/nv414 PMID: 26352255

4. Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, et al. (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecology letters 14: 101–112. doi: 10.1111/j.1461-0248.2010.01559.x PMID: 21087380

5. Richardson JS, Naiman RJ, Swanson FJ, Hibbs DE (2005) Riparian communities associated with pacific northwest headwater streams: assemblages, processes and uniqueness. Wiley Online Library.

6. Tagwiireyi P, Sullivan SMP (2015) Riverine Landscape Patch Heterogeneity Drives Riparian Ant Assemblages in the Scioto River Basin, USA. PLoS one 10: e0124807. doi: 10.1371/journal.pone.0124807 PMID: 25894540

7. Gray CL, Lewis OT, Chung AY, Fayle TM (2015) Riparian reserves within oil palm plantations conserve logged forest leaf litter ant communities and maintain associated scavenging rates. Journal of Applied Ecology 52: 31–40. doi: 10.1111/1365-2664.12371 PMID: 25678717

8. Ives CD, Hose GC, Nipperess DA, Taylor MP (2011) Environmental and landscape factors influencing ant and plant diversity in suburban riparian corridors. Landscape and Urban Planning 103: 372–382.

9. Lopes JFS, Hallack NMDR, Sales TA, Brugger MS, Ribeiro LF, Hastenreiter IN, et al. (2012) Comparison of the Ant Assemblages in Three Phytophysionomies: Rocky Field, Secondary Forest, and Riparian Forest—A Case Study in the State Park of Itibipoca, Brazil. Psyche: A Journal of Entomology 2012.

10. Johnson JT, Adkins JK, Rieske LK (2014) Canopy Vegetation Influences Ant (Hymenoptera: Formicidae) Communities in Headwater Stream Riparian Zones of Central Appalachia. Journal of Insect Science 14: 237. doi: 10.1093/jisesa/iue099 PMID: 25528753

11. Marczak LB, Sakamaki T, Turvey SL, Deguise I, Wood SL, Richardson JS, et al. (2010) Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecological Applications 20: 126–134. PMID: 20349835

12. Bennett AF, Nimmo DG, Radford JQ (2014) Riparian vegetation has disproportionate benefits for landscape-scale conservation of woodland birds in highly modified environments. Journal of applied ecology 51: 514–523.

13. Pérez-Toledo GR, Valenzuela-González JE, Flores-Galván C, Gallardo-Hernández C, Vázquez-Torres V, García-Martínez MA (2016) Hormigas (Hymenoptera: Formicidae) asociadas a tres tipos de vegetación de un paisaje agropecuario en Veracruz. Entomología Mexicana 3: 582–588.

14. Corbacho C, Sánchez JM, Costillo E (2003) Patterns of structural complexity and human disturbance of riparian vegetation in agricultural landscapes of a Mediterranean area. Agriculture, Ecosystems & Environment 95: 495–507.

15. Fernández D, Barquin J, Álvarez-Cabria M, Peñas FJ (2014) Land-use coverage as an indicator of riparian quality. Ecological Indicators 41: 165–174.

16. Martin TG, McIntyre S, Catterall CP, Possingham HP (2006) Is landscape context important for riparian conservation? Birds in grassy woodland. Biological Conservation 127: 201–214.

17. Rodríguez-Mendoza C, Pineda E (2010) Importance of riparian remnants for frog species diversity in a highly fragmented rainforest. Biology letters 6: 781–784. doi: 10.1098/rsbl.2010.0334 PMID: 20554561

18. Galindo-González J, Sosa VJ (2003) Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. The Southwestern Naturalist 48: 579–589.

19. Didham RK (2010) Ecological consequences of habitat fragmentation. eLS.

20. Alonso LE, Agosti D (2000) Biodiversity studies, monitoring, and ants: an overview. In: Agosti D, Majer JD, Alonso LE, Schultz TR, editors. Standard methods for measuring and monitoring biodiversity. Washington DC: Smithsonian Institution. pp. 1–8.

21. Andersen AN, Hoffmann BD, Müller WJ, Griffiths AD (2002) Using ants as bioindicators in land management: simplifying assessment of ant community responses. Journal of Applied Ecology 39: 8–17.

22. Underwood EC, Fisher BL (2006) The role of ants in conservation monitoring: if, when, and how. Biological conservation 132: 166–182.

23. Gollan JR, De Bruyn LL, Reid N, Smith D, Wilkie L (2011) Can ants be used as ecological indicators of restoration progress in dynamic environments? A case study in a revegetated riparian zone. Ecological Indicators 11: 1517–1525.

24. García-Martínez MÁ, Martínez-Tlapa DL, Pérez-Toledo GR, Quiroz-Robledo LN, Valenzuela-González JE (2016) Myrmecofauna (Hymenoptera: Formicidae) response to habitat characteristics of tropical montane cloud forests in central Veracruz, Mexico. Florida Entomologist 99: 248–256.
25. Silvestre R, Demétrio MF, Delabie JHC (2012) Community structure of leaf-litter ants in a Neotropical dry forest: a biogeographic approach to explain biodiversity. Psyche: A Journal of Entomology 2012.

26. Wilson EO, Hölldobler B (2005) The rise of the ants: a phylogenetic and ecological explanation. Proceedings of the National Academy of Sciences of the United States of America 102: 7411–7414. doi: 10.1073/pnas.0502264102 PMID: 15899976

27. Silva RR, Brandão CRF (2010) Morphological patterns and community organization in leaf-litter ant assemblages. Ecological Monographs 80: 107–124.

28. Ries L, Fletcher RJ Jr, Battin J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics: 491–522.

29. Perfecto I, Vandermeer J (2002) Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. Conservation Biology 16: 174–182.

30. Spiesman BJ, Cumming GS (2008) Communities in context: the influences of multiscale environmental variation on local ant community structure. Landscape Ecology 23: 313–325.

31. De la Mora A, Murnen C, Philpott S (2010) Morphological patterns and community organization in leaf-litter ant assemblages. Ecological Monographs 80: 107–124.

32. Crist TO (2009) Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review. Myrmecological News 12: 3–13.

33. Woodcock P, Edwards DP, Fayle TM, Newton RJ, Khen CV, Bottrell SH, et al. (2011) The conservation value of South East Asia’s highly degraded forests: evidence from leaf-litter ants. Philosophical Transactions of the Royal Society of London B: Biological Sciences 366: 3256–3264. doi: 10.1098/rstb.2011.0031 PMID: 22006966

34. Williams-Linera G, Manson RH, Isunza-Vera E (2002) La fragmentación del bosque mesofilo de montaña y patrones de uso del suelo en la región oeste de Xalapa, Veracruz, México. Madera y bosques 8: 73–89.

35. Dauber J, Purtauf T, Allspach A, Frisch J, Voigtländer K, Wolters V (2005) Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. Global Ecology and Biogeography 14: 213–221.

36. Muñoz-Villers L, López-Blanco J (2008) Land use/change changes using Landsat TM/ETM images in a tropical and biodiverse mountainous area of central-eastern Mexico. International Journal of Remote Sensing 29: 71–93.

37. López-Barrera F, Landgrave R (2008) Variación de la biodiversidad a nivel paisaje. In: Manson RH, Hernández-Ortiz V, Gallina S, Mehltreter K, editors. Agroecosistemas cafetaleros de Veracruz: Instituto de Ecología—Instituto Nacional de Ecología. pp. 259–269.

38. Rempel RS, Kaukinen D, Carr AP (2012) Patch analyst and patch grid. Ontario Ministry of Natural Resources Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.

39. Patton DR (1975) A diversity index for quantifying habitat “edge”. Wildlife Society Bulletin (1973–2006) 3: 171–173.

40. Guérand B, Lucky A (2011) Shuffling leaf litter samples produces more accurate and precise snapshots of terrestrial arthropod community composition. Environmental entomology 40: 1523–1529. doi: 10.1603/EN11104 PMID: 22217769

41. Mackay WP, Mackay E. Clave de los géneros de hormigas en México (Hymenoptera: Formicidae). In: Quiroz-Robledo LN, Garduño-Hernández LM, editors; 1989; Oaxtepec, Morelos, Mexico. Sociedad Mexicana de Entomología. pp. 1–82.

42. Branstetter MG (2013) Revision of the Middle American clade of the ant genus Stenamma Westwood (Hymenoptera, Formicidae, Myrmicinae). ZooKeys: 1.

43. Longino JT (2007) Ants of costa rica. URL: http://academicevergreenedu/projects/ants/genera/stegomyrmex/species/manni/manni.html, accessed in July 24: 2007.

44. Longino JT (2012) A review of the ant genus Adelomyrmex Emery 1897 (Hymenoptera, Formicidae) in Central America. Zootaxa 3456: 1–35.

45. Longino JT (2013) A review of the Central American and Caribbean species of the ant genus Eurhopalothrix Brown and Kempf, 1961 (Hymenoptera, Formicidae), with a key to New World species. Zootaxa 3693: 101–151. PMID: 26185839

46. Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93: 2533–2547. PMID: 23431585

47. Chao A, Gotelli NJ, Hsieh T, Sander EL, Ma K, Colwell RK, et al. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45–67.
48. Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution.

49. Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54: 427–432.

50. Jost L (2006) Entropy and diversity. Oikos 113: 363–375.

51. Jost L (2010) The relation between evenness and diversity. Diversity 2: 207–232.

52. Cumming G, Fidler F, Vaux DL (2007) Error bars in experimental biology. The Journal of cell biology 177: 7–11. doi: 10.1083/jcb.200611141 PMID: 17420288

53. Magurran AE (2004) Measuring biological diversity. Blackwells. Oxford, UK.

54. Clarke KR, Gorley RN (2006) User manual/tutorial. PRIMER-E Ltd, Plymouth.

55. Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366: 56–69.

56. Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach: Springer Science & Business Media.

57. Calcagno V, de Mazancourt C (2010) gmult: an R package for easy automated model selection with (generalized) linear models. Journal of Statistical Software 34: 1–29.

58. Barbosa AM, Brown JA, Jiménez-Valverde A, Real R (2014) modEvA: Model Evaluation and Analysis. R package, version 132.

59. Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for Primer. Plymouth, UK: Primer-E.

60. Clarke K, Warwick R (2005) Primer-6 computer program. Natural Environment Research Council, Plymouth.

61. Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, et al. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30: 609–628.

62. Bivand R, Altman M, Anselin L, Assunção R, Berke O, Bernat A, et al. (2016) spdep: Spatial Dependence: Weighting Schemes, Statistics and Models. R package version 0.6–8. https://cran.r-project.org/web/packages/spdep/index.html Dec 2016.

63. Goslee S, Urban D (2015) ecodist: Dissimilarity-based functions for ecological analysis. R package version 1.2.9. https://cran.r-project.org/web/packages/ecodist/index.html Accessed Dec 2016.

64. Lichstein JW (2007) Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecology 188: 117–131.

65. Milford ER (1999) Ant communities in flooded and unflooded riparian forest of the middle Rio Grande. The Southwestern Naturalist: 278–286.

66. Wilson MC, Chen X-Y, Corlett RT, Didham RK, Ding P, Holt RD, et al. (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landscape Ecology 31: 219–227.

67. Sobrinho TG, Schoereder JH, Sperber CF, Madureira MS (2003) Does fragmentation alter species composition in ant communities (Hymenoptera: Formicidae)? Sociobiology 42: 329–342.

68. Dauber J, Bengtsson J, Lenoir L (2006) Evaluating Effects of Habitat Loss and Land-Use Continuity on Ant Species Richness in Seminatural Grassland Remnants. Conservation Biology 20: 1150–1160. PMID: 16922331

69. Debuse VJ, King J, House AP (2007) Effect of fragmentation, habitat loss and within-patch habitat characteristics on ant assemblages in semi-arid woodlands of eastern Australia. Landscape Ecology 22: 731–745.

70. Herrera-Rangel J, Jiménez-Carmona E, Armbrrecht I (2015) Monitoring the Diversity of Hunting Ants (Hymenoptera: Formicidae) on a Fragmented and Restored Andean Landscape. Environmental entomology 44: 1287–1298. doi: 10.1093/ee/nvv103 PMID: 26314006

71. Murgueitio E, Calle Z, Uribe F, Calle A, Solorio B (2011) Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. Forest Ecology and Management 261: 1654–1663.

72. Semlitsch RD, Bodie JR (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17: 1219–1228.