



Original Articles

Using landscape composition and configuration metrics as indicators of woody vegetation attributes in tropical pastures

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ABSTRACT

Seasonally dry tropical forests in the Neotropics are typically transformed into pasture-dominated landscapes that represent a major threat to habitat biodiversity. Developing alternative management strategies that minimize the loss of native biota in agricultural landscapes is crucial. In a fragmented landscape in Veracruz, Mexico, we analyzed the community attributes of woody vegetation present in pastures in which different types of arboreal elements are common. We hypothesized that different landscape patterns, distinguishable using GIS land-cover maps, would be linked to woody plant diversity and its spatial variation. We created a detailed map of our study area distinguishing six forest cover types. We sampled the woody vegetation within 16 circular plots (100 m radius) each centered on an isolated fig tree and that varied in the amount of arboreal cover and proximity to remnant forest. We used a multimodel-inference approach to assess the relationship between different landscape metrics and woody vegetation response variables. Forest cover within each plot ranged from 3% to 44%. A total of 1777 woody plants (density = 35.4 plants ha⁻¹), belonging to 88 species were recorded. Landscape composition and configuration metrics, particularly the type and amount of arboreal cover, were strong indicators of woody plant richness and abundance, while landscape structural heterogeneity was strongly related to floristic composition. In contrast proximity metrics were weak explanatory variables. Tall canopy forest fragments and isolated trees explained most of the variation in richness and abundance. Results suggest that maintaining 20–40% woody cover within pastures and maximizing the heterogeneity of arboreal elements promotes the conservation of biodiversity in rural landscapes dedicated to livestock. Further, easily obtained landscape metrics can be used as a tool to enhance vegetation assessment and help in the development of more convenient management practices that seek to increase native species richness, while improving landscape connectivity and resilience.

1. Introduction

Seasonally Dry Tropical Forests (SDTF; *sensu* Pennington et al., 2009) are one of the most threatened habitat types in the world, largely due to anthropogenic disturbance (Chazdon et al., 2011). In the Neotropics less than 10% of the original extent of this forest type remains (DRYFLOR, 2016). SDTF in Latin America has been subjected to intense agricultural transformation for centuries, leading to the formation of human-dominated ecosystems. Pasture is the predominant land use in the human-modified landscapes of the Neotropics and is replacing once extensive tropical forest (Chazdon, 2014). In spite of being pasture-dominated, these landscapes often retain some interspersed tree cover

(hereafter ‘arboreal landscape elements’), which can play a fundamental role in conserving remaining biodiversity (Chazdon et al., 2011; Guevara et al., 2005; Harvey et al., 2011), making it impossible to keep regarding the matrix as devoid of trees.

Complex, structured matrices are essential for enhancing and maintaining a greater number of resources and ecological processes, increasing landscape connectivity, and are a form of insurance that guarantees resilience in rural landscapes when they are managed properly (Guevara et al., 2005; Harvey et al., 2006; Ricketts, 2001). Pastures that include trees can be considered a type of agroforestry system that is traditionally managed, with a high degree of structural heterogeneity and a wide variety of physiognomies (Broom et al.,

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2013). Usually, scattered trees standing in the middle of crop-fields or grazing lands form part of the agricultural and cattle ranching practices in Mexico (Guevara et al., 2005) and Central and South America (Harvey et al., 2011; Siqueira et al., 2017). Despite their potential value for biodiversity conservation, there are still few rigorous descriptions of tree cover configuration and its associated properties, particularly those evaluating the community attributes and species composition of woody plants in tropical and subtropical rural landscapes dominated by pastures.

Traditional approaches to studying fragmented landscapes typically assume a framework based on island biogeography and/or meta-population theory, focusing on the fragments themselves and ignoring the surroundings. This framework relegates the deforested matrix to that of a uniform non-habitat that surrounds remnant patches of habitat (the habitat matrix paradigm; *sensu* Manning, et al., 2006; Ricketts, 2001). The matrix is often considered a barren artificial barrier that is even deleterious for native forest biota, without having made any attempt to describe its structure and composition (*but see* Doubrava et al., 2013; Guevara et al., 1998, 2005; Mendenhall et al., 2011, 2012; Johnson et al., 2015). This patch-centric view, prevalent in many landscape ecology studies, usually misses the finer details of the matrices and the important role that they may have in landscape function.

Given that ~75% of the planet's ecosystems are strongly affected by human activity, and only 13% are in protected areas (Mendenhall et al., 2013), developing a more complete conservation framework that incorporates the finer characteristics of the landscape matrix is necessary to study biodiversity changes in human-modified landscapes. A first step is to develop accurate and quantitative descriptors of the structural attributes and species composition of the arboreal elements present within active tropical pastures, which would allow us to improve management in these landscapes. Incorporating biodiversity conservation plans in tropical agricultural landscapes is an important strategy that should go hand in hand with the implementation of more resilient and sustainable livestock management systems (Guevara et al., 1998; Harvey et al., 2006).

For the design and execution of conservation plans in human-modified landscapes, the assessment of the spatial configuration and vegetation attributes of arboreal elements present within such habitats should be practical and easy to carry out. Landscape patterns can be characterized utilizing metrics such as geometry, structure, or degree of isolation of the elements that form the landscape (McGarigal et al., 2012). Remote sensing and spectral or textural information have been used to predict vegetation structure (Block et al., 2016; Gallardo-Cruz et al., 2012; Wood et al., 2012), however, in many cases the spatial resolution employed is not fine enough to reveal all of the trees present within pastures, and few studies perform ground verification to determine the arboreal species composition. In fragmented landscapes, factors operating at the landscape level such as remnant forest area and land cover heterogeneity could be related to biological community attributes, as found in different studies in which structural landscape metrics have been reported as biodiversity predictor variables for distinct groups of animals and plants (Carrara et al., 2015; Collins and Fahrig, 2017; Häger et al., 2014; Hernández-Stefanoni and Dupuy, 2008; Torras et al., 2008).

In this study, we assess whether easily obtainable metrics of landscape composition and configuration, degree of isolation, and heterogeneity – as estimated through a land cover map derived from remote sensing data – can be used as indicators of the attributes of the woody vegetation found in a pasture-dominated matrix in Veracruz, Mexico. In addition, we seek to characterize their spatial variation and woody species composition on the landscape. We focus on three goals: 1) to determine the extent to which community attributes of woody vegetation found within pastures, and their spatial variation, can be explained by landscape patterns revealed by remote sensing data; 2) to assess the relative contribution of different landscape elements as indicators of high woody vegetation diversity; 3) to describe the

structural and floristic attributes of the woody vegetation present within active pastures, and assess the magnitude of its spatial variation under different scenarios of deforestation. Our study seeks to improve and support the assessment of tree species communities in rural landscapes as part of new management and conservation strategies that can lead to improved maintenance of ecosystem function and resilience in these agro-silvopastoral systems.

2. Methods

2.1. Study area

The study was conducted in a fragmented landscape with a long history of agricultural use in the tropical lowlands of the state of Veracruz, Mexico, within the municipality of Jamapa (18°55'–19°04'N and 96°10'–96°19'W). The area is part of the coastal plain of the Papaloapan River Basin and ranges in elevation from 10 to 40 m a.s.l. Mean annual temperature is 24–26 °C, and mean annual rainfall is 1100–1300 mm/yr (INEGI, 2009). Precipitation is strongly seasonal with a marked rainy season from June to September (> 200 mm/mo) and a dry season from October to May (< 100 mm/mo); January to April are the driest months (< 20 mm/mo) (CLIMATE-DATA ORG, 2018).

This region, once covered by extensive SDTF interspersed with wetlands and palm groves, has been altered and maintained for different agricultural uses since pre-Hispanic times (Escamilla-Perez, 2013). At present, the dominant type of land use is man-made pastures to raise cattle, which is the main agricultural activity across the entire coastal plain of Veracruz (Fig. S.1 in Supplementary material). Nonetheless, in the rural landscape of Jamapa farmers leave different arboreal elements standing in pastures as a source of firewood, timber, complementary fodder, fences, and as shade for livestock, with a notable density of isolated shade trees (Lazos-Ruiz et al., 2016). Some of these arboreal elements are remnants of the original forest canopy or sub-canopy, but many others established naturally or were planted after the forest conversion to pasture.

The two largest remnant patches of old-growth forest with a relatively continuous canopy > 15 m that have been preserved by locals in our study area are known as El Palmar and El Apompal (Fig. 1). The former is a remnant forest patch 89.2 ha in area, dominated by the palms *Roystonea dunlapiana* and *Attalea butyracea*. The latter is a floodable forest patch 56.4 ha in area surrounding the Apompal Lagoon (30 ha) and is dominated by *Pachira aquatica* with an abundance of *R. dunlapiana* and *A. butyracea* palms (Escamilla-Perez, 2013). Our study area was delimited using these two fragments of remnant forest as centroids and by merging two circumferences with a 6 km radius centered around each remnant (total study area 20,070 ha).

2.2. Land cover map

We created a land cover map of our study area (Fig. 1) using high resolution (1 m/pixel) aerial ortho-photographs taken in 2007 and 2008, together with a digital elevation model (DEM) provided by INEGI (2009). The latter, had a resolution of 5 m/pixel and was derived from the interpolation of LIDAR data (211 pulses/ha) by INEGI (see Appendix C for more details). We also used geo-referenced vector maps of the area that highlighted rivers, water bodies, roads and towns (INEGI, 2009). All pixels with a vegetation height ≥ 2.5 m (i.e., difference between the terrain and surface digital models, from the DEM) were classified as “forest cover”; remaining areas were classified as “non-forest cover”. The raster map was converted into a vector shapefile, from which all polygons with an area < 70 m² were merged with the surrounding background area (to simplify polygons). The “forest cover” category was further sub-divided into six classes based on canopy height, patch area, and the shape of each polygon. Polygons were delimited and classified, with decisions supported by visual

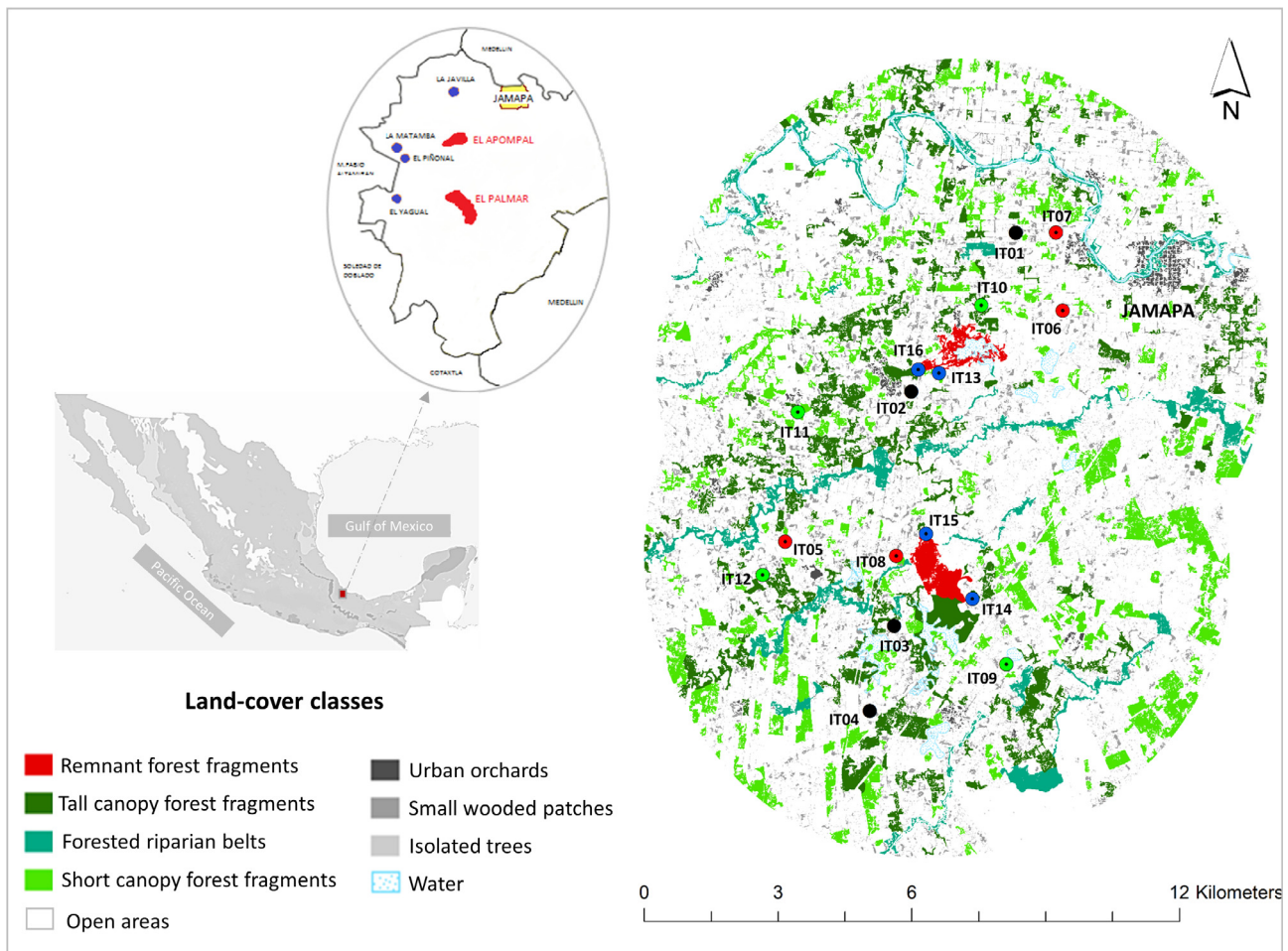


Fig. 1. Land cover map of the study area in Jamapa, Veracruz, Mexico. The area was centered on the two largest old-growth remnants of SDTF in the region: El Apompal (56.4 ha) and El Palmar (89.2 ha). The nine land-cover classes shown are described in detail in Table 1. The location of the 16 sampling units, each centered on an isolated fig tree, are indicated by a colored circle (IT01–IT16). The color category represents one of the four land-use intensity scenarios described in Section 2.3 (scenario I black; II red; III green; and IV blue).

Table 1

Land cover classes distinguished in the entire study area in Jamapa, Veracruz, Mexico (depicted in Fig. 1), showing total area per class, patch size range (minimum and maximum patch) per class, and percent cover of total area.

Land-cover class	Tot. area (ha)	Size range (ha)	% tot. area	Description
<i>Tall canopy forest fragments</i>	1597	1.3–61.1	8.0%	Forest fragments > 1 ha with a closed-canopy ≥ 10 m tall (including the two remnant forest fragments of the next sub-class, below)
<i>Remnant forest fragments</i>	146	56.4 and 89.2	0.7%	Old growth primary forest, with a canopy ≥ 15 m tall. Two remnants: El Apompal and El Palmar
<i>Forested riparian belts</i>	701	0.16–107.4	3.5%	Elongated fragments of arboreal belts associated with rivers
<i>Short canopy forest fragments</i>	1702	1.2–58.3		Patches of secondary forest > 1 ha, with a discontinuous or closed canopy ≥ 2.5 m and < 10 m tall
<i>Urban orchards</i>	138	–	0.7%	Arboreal patches within settlements
<i>Small wooded patches</i>	631	0.15–1.0	3.1%	Scattered tree clusters with canopy height ≥ 2.5 m and area ≥ 0.15 but ≤ 1 ha, that could be arranged as shelterbelts or living fences
<i>Isolated trees</i>	716	0.001–0.15	3.6%	Individual remnant or planted trees (area ≤ 0.15 ha) scattered within pastures or crop-fields
<i>Open areas (with no woody cover)</i>	14,318	–	71.3%	Active pastures, crop fields, human infrastructure, or denuded sites (e.g. roads, houses, bare ground, etc.)
<i>Water</i>	267	–	1.3%	Water; including rivers, ponds, and reservoirs

interpretation (1:2000), in ArcMap 10.2.2 (ESRI, 2014), and then ground-truthed. A description of each land cover class is provided in Table 1.

The degree of accuracy of our classification process was estimated using a total of 669 selected ground verification points associated with different land-cover types (except the water class). Data from verification points were arranged in a confusion matrix (see Appendix C for more details) from which the overall accuracy of our map was

estimated, together with the Cohen-Kappa index of concordance, where values approaching 1 represent high accuracy and reliability (Cohen, 1960; Congalton et al., 1983).

2.3. Vegetation sampling

Isolated fig trees (*Ficus* spp.) are widespread in our study area, being highly preferred by ranchers as a source of shade for cattle. The

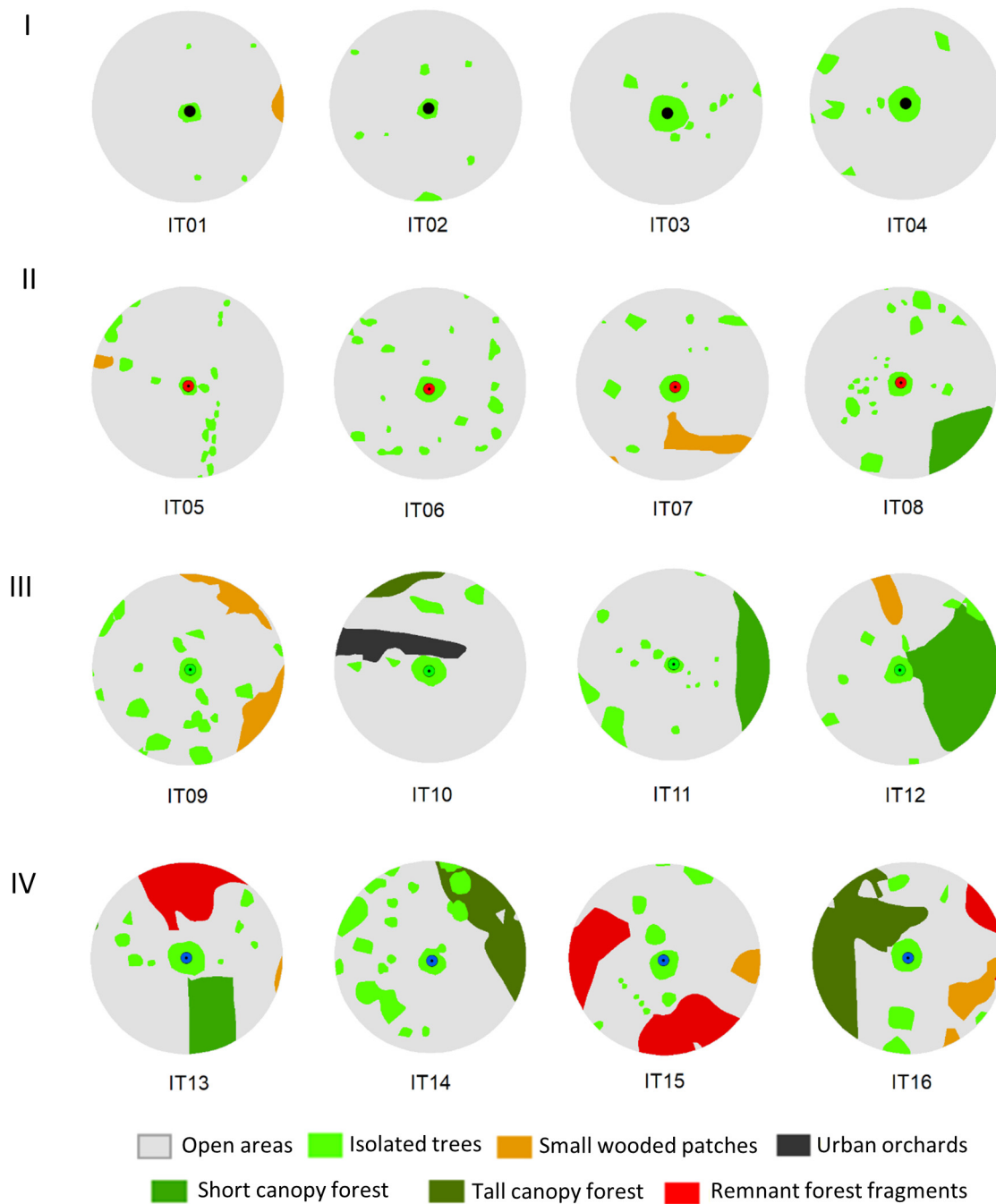


Fig. 2. Spatial structure of each of the 16 sampling units (circular plot = 3.1 ha) showing open areas and the forest cover classes (see Table 1) present within each plot. Each row corresponds to one of the four land use intensity scenarios arranged from the simplest, with highest disturbance intensity (scenario I; top row) to the most complex one, with lowest disturbance intensity (IV; bottom row).

strangler fig *F. cotinifolia* is typical of the canopy of the original SDTF and is the most common species, representing 89% of 183 fig trees censused within pastures of our study area. We selected sixteen isolated trees of this species as focal points for sampling the woody vegetation, choosing individual trees that were relatively large (> 15 m in height) and therefore likely remnants of the original forest canopy. For each sampling unit, a circular plot with a 100 m radius (3.1 ha) was established, centered on one of the *F. cotinifolia* trees selected. In addition to belonging to this species and being also a relatively large tree, selection of a focal Isolated Tree (IT) was based on two additional criteria: 1) the IT had to be located at different distances from any of the two large remnant old-growth SDTF, and 2) the amount of surrounding forest cover quantified (100 m radius) had to differ in order to have an ample

gradient among sampling units. Focal plot separation ranged from 275 to 11,363 m.

The 16 plots sampled were grouped into four contrasting habitat scenarios (n = 4 plots per scenario; Fig. 2). The four land use intensity scenarios were: I) minimal forest or arboreal cover (< 6%); II) scant forest cover (6–15%); III) intermediate forest cover (15–37%); and IV) abundant forest cover (30–45%). The latter category had its central fig located relatively close (i.e., < 150 m) to one of the two large remnant fragments, whereas the remaining three scenario plots had their respective plot centers at least 300 m away from either of the two remnant fragments.

All woody plants with a diameter at breast height (dbh) ≥ 10 cm were recorded within the entire sampling unit (3.1 ha); smaller woody

plants with a dbh ≥ 5 cm were recorded in a nested sub-plot with a 50 m radius of each focal IT (0.8 ha). Data of the 100 m radius plot and its respective 50 m radius sub-plot were pooled without duplicating species counts per site. For each plant censused, we determined species and local name, and recorded dbh, distance and orientation (azimuth) with respect to their focal IT. Nomenclature follows Tropicos.org (2018). Specimens that could not be identified to the species level were treated as morpho-species in the analyses. At the time of vegetation sampling, all pastures were being actively grazed and subject to regular ranching practices of the area (i.e., clearing, use of chemical herbicides).

2.4. Data analysis

In order to characterize the landscape, we estimated different landscape metrics using ArcMap 10.2.2 (ESRI, 2014) and FRAGSTATS 4.0 (McGarigal et al., 2012) from our land cover map. To assess the degree of isolation of each of the 16 sampling plots at the landscape level, we estimated the nearest distance between each focal IT and each of three forest cover classes: old-growth remnant (D_remn), riparian forest belt (D_rip), and forest or arboreal fragment > 1 ha (D_fragment). To analyze landscape attributes within each sampled unit (i.e., plot-level variables), a circular area with a 100 m radius centered on each focal IT was plotted in ArcMap. Within this area, the following composition metrics were estimated: percentage of total forest cover (FORCOV), mean area of forested patches (i.e., polygons) weighted by area (AREA_AM), and percent cover by forest type or class. Configuration metrics included: total length of all forest edges within the circular plot (ED); and patch density (NP/ha), defined as the number of forested patches standardized by the area of each plot. Landscape heterogeneity was estimated with the Shannon diversity index (SHDI) taking into account the proportion of the sampling unit occupied by each patch type or forest cover class. See McGarigal et al. (2012) for a detailed description of each metric (see metric values *per* sampling unit in Table A.1 in Appendices). We selected metrics that are easiest to obtain and interpret, as well as those that have been persistently found to be related to plant species richness (Luoto, 2000), or reported as ecologically meaningful in fragmentation studies (Rutledge, 2003).

For each species recorded, an overall importance value index (IVI) was estimated using the formula and procedures described by Curtis and McIntosh (1951), and taking into account relative values of abundance, basal area, and frequency within the 16 plots sampled. Rank-abundance curves for each of the four scenarios were plotted. Similarity in species composition among scenarios was estimated using a Sørensen quantitative index (Magurran, 2004), and ANOSIM analysis. Analyses were performed using the *vegdist* function in the *vegan* package for R version 3.3.3 (Oksanen et al., 2017; R Core Team, 2017).

The spatial variation in species composition among plots, and its relationship to landscape metrics were analyzed with canonical correspondence analysis (CCA) using the *vegan* package (Legendre and Legendre, 2012; R Core Team, 2017), and Euclidean distance as the similarity measure and log-transformed abundance data. The optimal spatial arrangement of the 16 sampling plots was plotted as a 2-dimensional ordination diagram following standard procedures described in McCune et al. (2002). Landscape metrics whose values per plot had a squared correlation coefficient (r^2) > 0.3 with any of the two CCA axes (Table B.1, in Appendices) are shown as vectors in the ordination diagram. Species whose abundance were strongly correlated with any of the two CCA axes are also shown.

Species richness, species abundance, and basal area of woody plants for each of the 16 sampling plots were calculated (Table A.1). Deviance of generalized linear models (GLMs) was analyzed separately for each response variable to compare each among the four scenarios using the *stats* package for R (R Core Team, 2017). We assumed a Poisson error distribution and a log-link for richness, Quasi-Poisson error and a log-link for abundance data, and a Gaussian error distribution and an

identity-link for basal area. *Post hoc* contrast tests were performed (Crawley, 2013) to identify differences between scenarios using the *models* package for R (Warnes et al., 2015).

To analyze which landscape metric had the greatest effect on vegetation attributes we used an information-theoretic approach and multi-model inference, testing the relative importance and direction of explanatory variables separately on each response variable, and by making inferences from all the models in a candidate subset (Burnham and Anderson, 2002). To avoid the inclusion of auto-correlated landscape variables in a given model we used bi-variate GLMs and Pearson correlation coefficients for all metrics, following Timm et al. (2016). The variance inflation factor for all explanatory variables was also computed to avoid collinearity using the *car* package for R (Fox and Weisberg, 2011). Two independent GLM analyses were performed for isolation landscape-level variables (i.e., distance metrics to the nearest fragments) and for structural variables at the plot level (i.e., composition and configuration metrics). The Akaike Information Criterion corrected for small samples (AICc) was used to select the best models (Burnham and Anderson, 2002). Richness and abundance were assessed with the quasi-AICc (QAICc) in order to correct for the over-dispersion that is associated with count data (Calcagno, 2013).

A set of models was constructed representing all combinations of explanatory variables, constrained to a maximum of three per model. Models were ranked according to their AICc and delta values (Δ AICc), following Burnham et al. (2011), and using a cutoff value of Δ AICc < 2 for model selection (Burnham and Anderson, 2002). Additionally, the subset of models for which the sum of Akaike weights (Σw_i) was higher than 0.95 was considered to have 95% confidence of containing the best approximating model, and thus was also selected as the subset of top models (Whittingham et al., 2005). The Σw_i of each selected model, in which a given explanatory variable was included, was used to assess its relative importance (Burnham and Anderson, 2002). Weight values (w_i) of the top models subset were also used to produce model-averaged parameter estimates (β), whose sign and magnitude represent the direction and size of effect, respectively, of each explanatory variable on each of the three response variables. Because all best models of richness and abundance included the percentage of forest cover (FORCOV) within the plot as the strongest explanatory variable, a further analysis for each attribute was performed using the percent cover of forested classes recognized in this study (see Table A.1; Fig. 2). This was done to assess whether distinguishing the forest cover type would improve the explanatory power of the models. All models were built using the *glmulti* package for R (Calcagno, 2013).

A “leave one out cross-validation” (LOOCV) procedure (Picard and Cook, 1984; Stone, 1974) was performed to evaluate the predictive accuracy of each model as well as that of the averaged model derived from the subset of top models, using the *boot* package (Canty and Ripley, 2017) and the *MuMIn* package for R (Barton, 2018). The root mean squared error (RMSE) was calculated as the squared root of the average of the MSE obtained by each LOOCV iteration (James et al., 2013).

3. Results

A total of 14,318 ha (71%) of the entire study area (20,070 ha) were categorized as open areas with no woody cover and 267 ha were covered by water. The remaining 5485 ha (27%) correspond to the “forest cover” category (woody vegetation ≥ 2.5 m) that was differentiated into six classes (Table 1). The overall accuracy of the final land-cover map classification was 94%, and the Kappa coefficient was 0.93. Classes with the greatest accuracy were urban orchards, open areas, and isolated trees followed by forested riparian belts and small wooded patches, while the tall and short canopy forest classes had the lowest accuracy, albeit in all cases it was > 0.83 (Table C.1 in Appendix C).

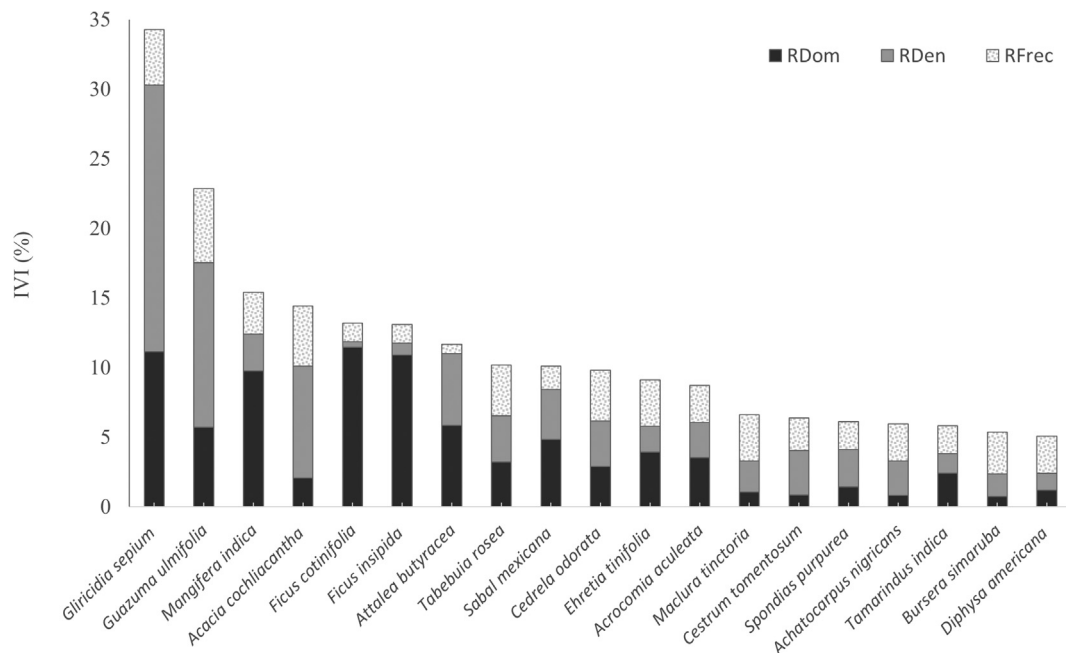


Fig. 3. Importance Value Index (IVI) of dominant species (> 5%) ranked from highest to lowest and pooled for all 16 sampling units. The contribution to IVI by relative dominance (RDom = basal area), density (RDen) and frequency (RFrec) per species is shown.

3.1. Community attributes of woody vegetation

A total of 1777 woody plants > 5 cm dbh, belonging to 88 species from 39 families, were recorded within the 16 sampling plots (total sampled area = 50.26 ha). Of these, the majority (1573 individuals) were large trees with dbh > 10 cm. Overall density of woody plants was 35.4 individuals ha⁻¹. Of the 88 species censused, 80 were identified to the species level, four to genus, and three to family; only one species was not identified. Fabaceae was the family best represented, accounting for 18% of total richness (16 spp.), followed by Moraceae (9 spp.), Arecaceae, and Boraginaceae (5 spp., each). The 20 most abundant species accounted for 81% of all individuals. Sixty-two species (71%) were represented by 10 or fewer individuals, including 11 doubletons and 21 singletons (see species list in Table D.1). In terms of plot-level presence, twelve species were recorded in half or more of the sampling units; *Guazuma ulmifolia* was the only species present in all 16 plots. The most abundant species was *Gliricidia sepium* (340 ind.), followed by *G. ulmifolia* (210 ind.) and *Acacia cochliacantha* (143 ind.). Most species (72.6%) are endo-zoochorous, 17.9% are anemochorous and 8.3% have a different dispersal syndrome (other). Only 19 species had an IVI > 5% and could be classified as dominant (Fig. 3). Of these, *G. sepium* and *G. ulmifolia* were the only ones with an IVI > 20%, however, species with IVI between 5 and 20% could be part of the canopy and sub canopy of old-growth forests.

Species richness, abundance and basal area per sampling unit are shown in Table A.1. Mean richness per plot was significantly different among scenarios ($X^2_{(3, 12)} = 39.5$; $p < 0.001$), being poorer in the simplest scenarios (i.e., I and II; < 15 spp./plot) and richest in the more complex scenarios (III and IV; > 20 spp./plot). Mean abundance per plot was significantly different among all four scenarios ($F_{(3, 12)} = 22.6$; $p < 0.001$), increasing steadily with lower landscape disturbance intensity (22.0 plants/plot scenario I vs. 234.0 plants/plot in scenario IV; $p < 0.05$). Even though basal area per plot also increased, only the least (I; 11.6 m²/plot) and most complex scenarios (IV; 85.6 m²/plot) differed significantly from each other ($X^2_{(3, 12)} = 17.9$; $p < 0.001$; Table 2).

3.2. Species composition analysis

Rank-abundance curves, pooled by scenario, indicate that only a few species dominated each scenario. The same two most dominant species as determined by IVI analysis were also dominant according to the rank-abundance curves. Additionally, *A. cochliacantha* and *Acrocomia aculeata* were dominant in at least three scenarios; other palms were amongst the most abundant in scenarios II and IV (Fig. 4). In scenarios III and IV, however, a notably higher number of species were rare (Fig. 4; Table D.1). Floristic composition varied among scenarios (ANOSIM; $p < 0.05$) in terms of their similarity values (Table 3). Scenarios III and IV had the highest similarity (0.53) with 39 species shared. Scenarios II and III had intermediate similarity (0.43), while remaining comparisons had lower values (< 0.33).

Ordination analysis showed a clear distinction in floristic composition between sampling units and scenarios (Fig. 5a). Total variance in the species data explained by the constrained ordination was 44%. Both CCA axes explained 22.5% of total cumulative variation in species composition, with 14.2% by axis 1 (eigenvalue 0.405) and 8.3% by axis 2 (eigenvalue 0.238). The CCA ordination roughly grouped sampling units of a given scenario closer together with the exception of scenario IV, whose plots were also largely separated from all other scenarios. CCA axis 2 represents a gradient from simpler (negative values) to more complex scenarios (positive values) in landscape structure and heterogeneity, and scenarios generally fit that pattern. CCA axis 1 grouping was less clear; placing plots with more cultivated species towards the left side of the CCA-plot, and those with more old-growth forest species to the right. The abundance of some species that are common in late successional stages or in old-growth forest were positively correlated with CCA axis 1. In contrast, the presence and abundance of cultivated species was negatively correlated with this axis (Fig. 5b). Of all the within-plot landscape metrics derived from our land cover map, FORCOV and SHDI both had the strongest positive correlation with CCA scores along axis 2 (Fig. 5a), whereas D.fragment > 1 ha and NP/ha both had a strongly negative correlation with this axis (Fig. 5a). D.rip had a strong negative correlation with axis 1 and a weaker positive correlation with axis 2 (Fig. 5a, see also Table B.1).

Table 2

Summary of vegetation attributes and landscape metrics pooled by scenario (Sc; n = 4 sampling units *per* scenario). Totals *per* scenario (in bold) and means (± 1 SD in italics) *per* plot for richness, abundance, and basal area of woody plants (different letters indicate significant differences between scenarios). For landscape metrics, either the mean (± 1 SD) or the range *per* scenario are shown as appropriate (see Section 2.4 for description of each metric). Values for each of the 16 sampling units are shown in Table A.1).

Attribute (or metric)	Sc I	Sc II	Sc III	Sc IV	Tot.
Richness (#spp)	29	31	50	71	89
Mean ± s.d./plot	10.8 ^a ± 3.4	13.8 ^a ± 2.6	22.3 ^b ± 3.4	27.8 ^b ± 7.0	18.6 ± 8.0
Abundance (#ind.)	88	263	490	936	1,777
Mean ± s.d./plot	22.0 ^a ± 11.8	65.8 ^b ± 29.7	122.5 ^c ± 20.3	234.0 ^d ± 86.1	111.1 ± 92.2
Basal area (m²)	11.6	23.2	67.6	85.8	188.2
Mean ± s.d./plot	2.9 ^a ± 2.2	5.8 ^{ab} ± 5.1	16.9 ^{ab} ± 11.4	21.5 ^b ± 7.0	11.8 ± 10.2
Landscape metrics ([range/plot]/mean ± s.d.)					
D_remn (m)	[455–2353]	[296–2800]	[429–3308]	[30–143]	[30–3308]
D_rip (m)	[484–1138]	[102–1250]	[424–1048]	[424–1143]	[102–1250]
D_fragment (m)	[216–566]	[102–1030]	[34–413]	[30–143]	[30–1030]
FORCOV (%)	[2.5–6.6]	[6.1–16.1]	[16.4–37.4]	[30.8–43.8]	[2.5–43.8]
AREA_AM (m ² /ha)	0.06 ± 0.04	0.07 ± 0.05	0.31 ± 0.27	0.38 ± 0.13	0.20 ± 0.20
ED (m/ha)	[65–168]	[243–322]	[206–383]	[312–441]	[65–441]
NP/ha (m/ha)	2.2 ± 0.6	5.3 ± 1.5	3.6 ± 1.1	4.0 ± 1.1	3.8 ± 1.5
SHDI	[0–0.68]	[0–0.73]	[0.62–0.99]	[0.68–1.13]	[0–1.13]

3.3. Spatial variation of vegetation attributes related to landscape metrics

In order to analyze whether both structural and isolation variables should contribute to the explanation of the response variables (i.e.,

woody plant attributes), we identified the most plausible models and the most important variables. Overall, the explanatory variables that best explained the spatial variation in woody vegetation attributes were those associated with landscape composition and configuration.

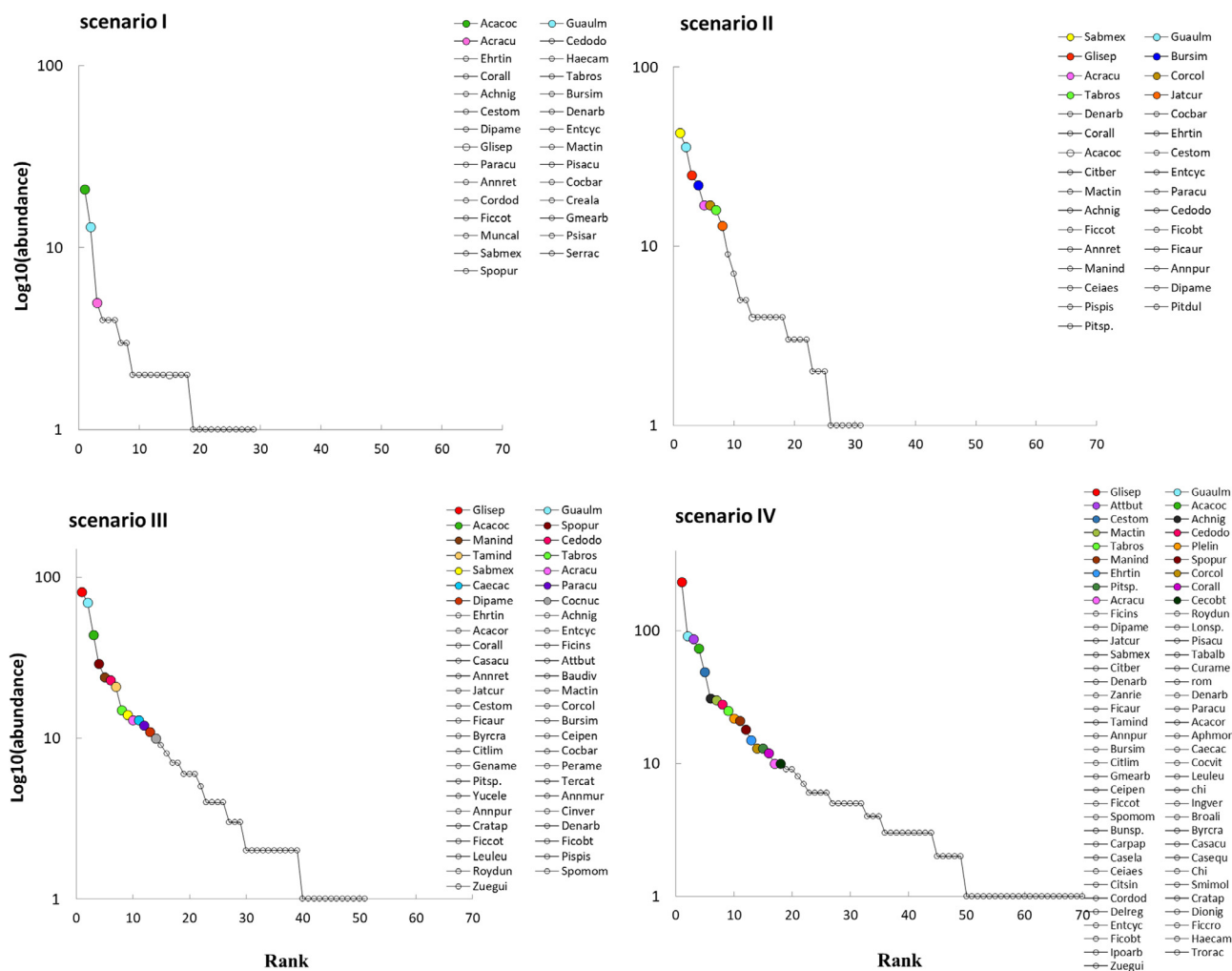


Fig. 4. Rank-abundance curves for each scenario, pooling the 4 sampling units for each one. Species are abbreviated using the first three letters of the genus and specific epithet; see full species names in Table D.1. Colored dots highlight species represented by 10 or more individuals (except in scenario I, where species ≥ 5 individuals are colored).

Table 3

Similarity in the species composition of woody species among the four land use intensity scenarios; showing the total number of species per scenario (bold numbers in diagonal grey boxes); number of shared species (*above the diagonal*) and similarity values, between each pair of scenarios (below the diagonal).

	Scen I	Scen II	Scen III	Scen IV
Scenario I	29	19	20	23
Scenario II	0.32	31	27	26
Scenario III	0.26	0.43	51	39
Scenario IV	0.15	0.28	0.53	71

Structural variables at the plot level (Fig. 6) had higher explanatory power for richness, abundance, and basal area than the isolation variables did (Table E.1). Models for basal area had much lower explanatory power than those of richness or abundance (Fig. 6; Table E.1). Based on model averaging, all structural plot-level variables were positively related to the three vegetation attributes, more strongly with richness and abundance. However, vegetation attributes were negatively and poorly related to isolation variables (Table E.2).

Species richness was best explained by the metric FORCOV ($\Sigma wi = 0.98$; Fig. 6a), which was included in all selected plausible models; whereas abundance of woody plants was best explained by FORCOV ($\Sigma wi = 1.00$) and NP/ha ($\Sigma wi = 0.51$; Fig. 6b). In turn, basal area was best explained by the density of the forest edge (ED; $\Sigma wi = 0.92$). It is important to note that ED was the main explanatory variable of basal area, but also was strongly and positively correlated with FORCOV, which is why the latter variable was not included in models for basal area (Tables E.1.b, and E.2.b). However, the unconditional variance of explanatory variables (except ED) of basal area models were usually greater than β (Table E.2), suggesting caution in the interpretation of the averaged model for this attribute (*sensu* Burnham and Anderson, 2002). Cross-validation (LOOCV) of the averaged subset of top-models for structural variables resulted in an estimated error (RSME) of ± 4.7 species per plot (15.7% of total range) for richness and ± 41.3 individuals per plot (11.8% of total range) for abundance. For isolation variables the error (RMSE) was almost twice as high (Table E.2.a) and thus much less accurate, than the models based on structural variables (Table E.2b).

When forest cover types were explicitly taken into account

(assessing the relative effect of each forest class) model selection results indicate that species richness and abundance are also explained by these within-plot metrics (79% and 92% of explained deviance, respectively; Fig. 7), while they are poorly related to basal area (< 30%). Cover percentage of tall canopy forest fragments (including the two large remnants; TFC + RF), was the strongest explanatory variable for species richness (Fig. 7a) and abundance (Fig. 7b). Other powerful explanatory variables for species richness and abundance were the percent cover of isolated trees pooled with the percent cover of small wooded patches (IT + SWP), as well as the percent cover of short canopy forest fragments (SFC). The most plausible model for species richness and for abundance includes the types of cover mentioned above (Table E.3). According to model averaging, those cover types are positively and strongly related to woody species richness and abundance (Table E.4). For the averaged model from the top-models subset distinguishing forest cover types, the estimated error (LOOCV-RSME) for richness was ± 6.4 spp./plot (21.4% of total range) and for abundance it was ± 54.3 ind./plot (15.6% of total range; Table E.4).

4. Discussion

Our study highlights the importance of arboreal elements within tropical pastures for the conservation of native flora in anthropic landscapes, as well as the potential of using structural landscape metrics—derived from image analysis and remote sensing data—as reliable indicators of the spatial distribution of woody plant species richness and abundance in highly deforested landscapes dominated by cattle pastures. Our results are important for the design and implementation of management tools within rural landscapes, aimed to promote biodiversity conservation without stopping livestock production.

4.1. The rural landscape of Jamapa: woody plants within active pastures

The deforestation of tropical forest in Jamapa and central Veracruz is very old, having begun long before the arrival of Europeans, when pre-hispanic slash-and-burn agriculture was extensively practiced in the area (Escamilla-Perez, 2013). After the conquest, the Spaniards introduced cattle in 1580 and more expansively in the early 1600 s when

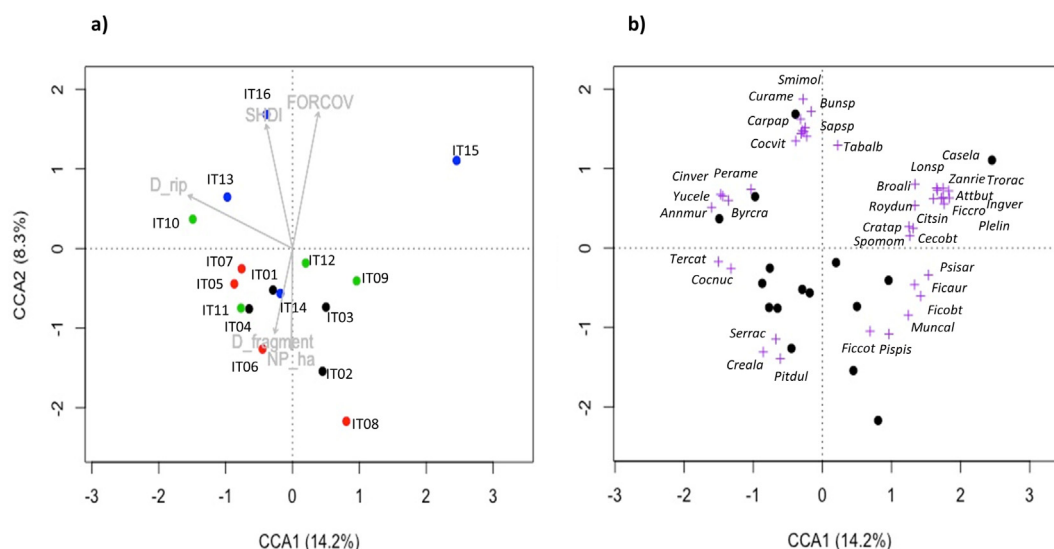


Fig. 5. CCA ordination analysis of the 16 sampling units (IT01 to IT16). Left panel (a) shows sample ordination as dots with different colors for each scenario: I (black), II (red), III (green) and IV (blue). Landscape metrics that had a relatively high correlation ($r^2 \geq 0.3$) with either of the two CCA axes are shown as vectors (length and direction of vector depicts the strength and direction of correlation; the angle is proportional to the correlation strength within a given axis; *sensu* McCune et al., 2002). The right panel (b) shows those species (indicated by a '+') whose incidence and abundance were strongly correlated with either of the CCA axes (species are abbreviated using the first three letters of the genus and the specific epithet; see Table D.1 in Appendices for full species names).

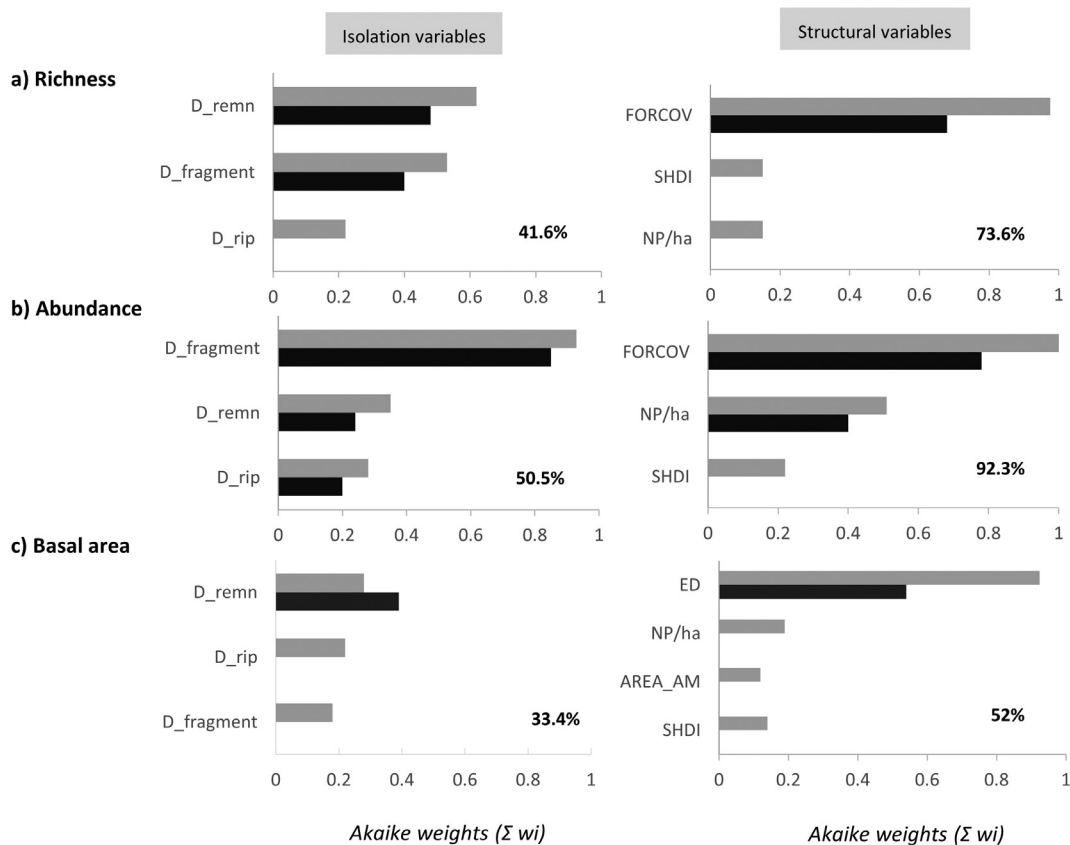


Fig. 6. Isolation (left) and structural (right) variables that best explain the spatial variation in vegetation attributes of the 16 units sampled for: Richness (a), Abundance (b), and Basal area (c). Variables shown are those included in the $\Delta AICc < 2$ set of models (black bars), and the $\Sigma wi > 0.95$ subset (grey bars). The sum of Akaike weights (Σwi) indicates the importance of each explanatory variable for each attribute modelled. Goodness of fit for each complete model is shown in the lower right side of each panel, as the percentage of explained deviance (Crawley, 2013).

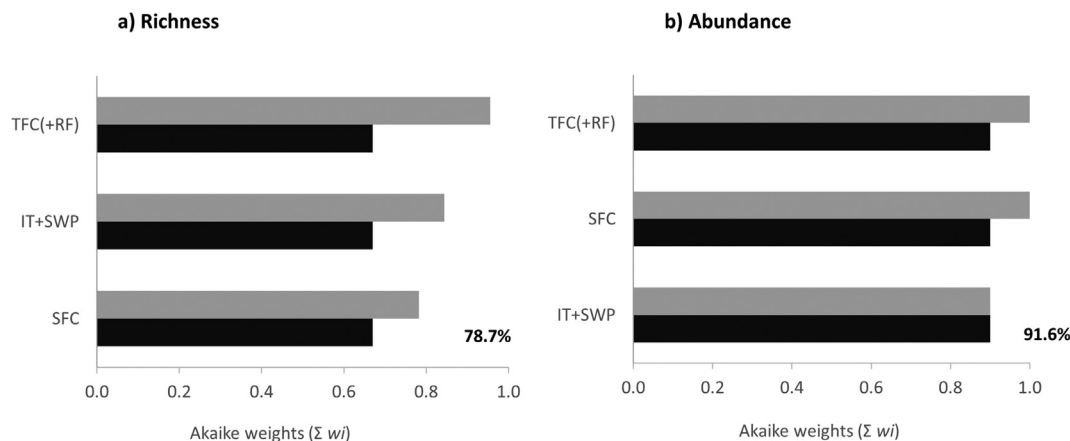


Fig. 7. Relative importance of the different types of forest cover classes present within sampling units as explanatory variables of richness (a) and abundance (b) of woody plants within each plot, that were included in the $\Delta AICc < 2$ set of models (black bars), and the $\Sigma wi > 95\%$ subset (grey bars). The sum of Akaike weights (Σwi) indicates the importance of each explanatory variable for each attribute. Goodness of fit of each complete model is shown at the lower right side of each panel, as the percentage of explained deviance (Crawley, 2013). Forest cover types are: TFC(+RF) (tall canopy forest, including the two remnant forest fragments); SFC (short canopy forest fragments pooled with urban orchards); and IT + SWP (isolated trees pooled with small wooded patches that include linear clusters of planted trees in living fences).

the first livestock permits (*estancias*) on the continent were granted throughout central Veracruz, including Jamapa (Sluyter, 1999). With the introduction of cattle, deforestation increased substantially and by 1950 more than 70% of the Jamapa area had been cleared.

Despite the considerable loss of forest and extensive habitat fragmentation, there are still forest or arboreal cover patches of different sizes and canopy heights in the region (Fig. 1). Remnant fragments, tall

canopy forest fragments and riparian belts represent the most durable arboreal elements in the landscape today and are the richest in tree species, containing the largest and tallest trees, with some taller than 15 m, though they only occupy a small fraction (< 9%) of the study area (Table 1). They represent the oldest secondary and old-growth forest patches with some of the least disturbed arboreal canopies in the area. The short canopy fragment class (< 10 m) corresponds to

relatively young secondary forest, and are the most dynamic arboreal elements of the landscape, since they are usually reconverted to pasture or crop-fields within a short period of time (see Reid et al., 2018). However, when left uncut they grow taller and richer in tree species (Chazdon, 2014). Finally, living fences and isolated trees, occurring at different densities within pastures, are not usually detected in low resolution images (e.g. Landsat with 25 m/pixel resolution) or they are ignored by researchers when digitizing their study areas. These landscape elements are, however, easily detected in higher resolution images (≤ 5 m/pixel) and in Jamapa's landscape they represent the most common types of arboreal element widely spread throughout the pastures of the area (Fig. 1). These findings suggest that forest regeneration through secondary succession is still occurring in the area alongside the selective removal or promotion of some woody species by farmers.

Due to the long history of deforestation, agricultural use, and hyper fragmentation in the area we expected to quantify only a handful of tree species, mostly fast-growing heliophiles that are highly competitive and typical of highly disturbed sites that have undergone floristic homogenization (Arroyo-Rodríguez et al., 2013). To our surprise, we found more than 80 species of woody plants in the active pastures of Jamapa in the ca. 50 ha sampled (Table D.1). The latter is within the range of 70–140 species of woody plants that has been reported for several pasture-dominated landscapes in the Neotropics, particularly in Central America (Harvey et al., 2011; Villanueva et al., 2004) and southern Mexico (Grande et al., 2010; Guevara et al., 2005; Villanueva-Partida et al., 2016).

Most of the species recorded (83%) are typical of SDTF; of these some ($\approx 25\%$) are also very common in rural vegetation or open areas including pastures. The remaining 17% are species that are only found in highly disturbed secondary vegetation habitat, where they can reach very high densities, or they are introduced and cultivated in the area (Castillo-Campos and Travieso-Bello, 2006). Dominant species (IVI > 20%) in the pastures of Jamapa include tree species that are widespread in Mexican, Central American and Colombian pastures, such as *G. sepium* and *G. ulmifolia*, both of which are highly favored by cattle ranchers (Harvey et al., 2011; Guevara et al., 2005; Siqueira et al., 2017; Villanueva-Partida et al., 2016), indicating that there is a high potential for floristic homogenization in this landscape. However, our results also show that the other dominant species included some long-lived and persistent pioneers that commonly form part of the SDTF canopy, such as *F. cotinifolia* (IVI value did not include the focal IT), *Tabebuia rosea*, *Cedrela odorata*, *Maclura tinctoria*, *Bursera simaruba*, as well as some tree species that are part of the canopy of more mesic forests, such as *F. insipida* and *Ehretia tinifolia*. In the same way, small trees or shrubs common in the understory or sub-canopy of SDTF, such as *Achatocarpus nigricans*, *Diphysa americana*, and *Spondias purpurea*, were also important (Fig. 3). Likewise, several native species were also among the most common species in the pastures studied, including some late successional species of seasonally dry tropical areas. Moreover, several rare species detected in our study are natives of the original SDTF, such as *Brosimum alicastrum*, *Ceiba pentandra*, *Annona purpurea*, *Crataeva tapia*, and *Diospyros nigra* (Fig. 4). Together they account for a relatively high proportion of the richness detected, greatly increasing the floristic heterogeneity of the woody flora in our study site.

The persistence of a diversity of forest species within the old and extensive pastures of Jamapa indicates that rural landscapes could be important reservoirs of native woody flora and that their maintenance in the landscape should be favored more emphatically. The current distribution and species composition of arboreal elements within pastures is based mainly on agricultural decisions and not explicitly on biological conservation criteria. Thus, conservation strategies must be incorporated into pasture and cattle management practices, in order to maintain and increase the population size of key native forest species within the agricultural landscape, not only to conserve the diversity of

woody plants, but also to promote the ecosystem services that these species provide (Manning et al., 2006). For example, 73% of the recorded species are endo-zoochorous and provide an abundant diversity of edible fruit for vertebrate frugivores in the pastures studied. In addition, a preliminary analysis of the avifauna visiting the 16 focal isolated *F. cotinifolia* trees and their surroundings, censused 97 bird species (Cadavid-Florez, unpublished data), of which 34% are migratory. Furthermore, Jamapa is located within the corridor of North-American migratory birds in the lowlands of Veracruz, an area that has been extensively deforested making the presence of forested patches or isolated trees within pastures for these migrating species even more important.

4.2. Landscape metrics and woody vegetation attributes

Our multi-model inference results indicate that it is possible to assess key attributes of the community of woody plants present in active pastures by using easily obtainable landscape metrics as indicators of these attributes. Several findings can be highlighted; first, the proportion of the area that is covered by forested vegetation in a given pasture site, detected from high resolution images and remote sensing data, was the strongest explanatory variable of the richness and abundance of woody plants growing in that site. The performance of forest cover percentage in describing plant richness and abundance was similar to results of Hernández-Stefanoni and Dupuy (2008), who found a strong positive association between tree species density and the percentage of land of a given patch-type in a landscape. Second, our results show that landscape heterogeneity was also positively related to woody plant richness and abundance, being a strong indicator of plant species richness in highly modified anthropic landscapes, consistent with the findings of Brotons et al. (2005) and Stahlheber (2016). The effects of landscape patterns on plant communities have been studied mainly using a fragment- or patch-centered approach, however our results highlight that similar trends occur within the landscape matrix outside of forest fragments.

Proximity to the nearest forest fragment has been reported as a metric that is strongly tied to species richness (Hernández-Stefanoni, 2005). Nonetheless, in our study, the three isolation variables for proximity to forested fragments did not have the expected positive effect on vegetation attributes. For instance, sites that were less than 150 m away from the two largest remnants of the original SDTF (i.e., our scenario IV plots) were as rich in woody species as those more than 400 m away from remnant forest (some of them > 2 km away; scenario III plots). Thus, landscape composition and configuration (structural variables at the plot-level) better explained the spatial variation in species richness and abundance of woody plants in the fragmented landscape of Jamapa than did landscape-level isolation variables. Our results complement studies indicating that landscape composition and configuration affect plant diversity (Häger et al., 2014; Hernández-Stefanoni and Dupuy, 2008; Torras et al., 2008).

Our results also suggest that the metrics of landscape composition (in particular, percentage of forest cover) have a higher explanatory value than metrics of landscape configuration (such as proximity to large forest fragments) as indicators of species richness and abundance, a result that is consistent with those of other studies (Alvarado et al., 2017; Arroyo-Rodríguez et al., 2016; Hernández-Stefanoni and Dupuy, 2008). Nevertheless, different landscape configurations are also relevant to the spatial variation in species richness of woody plants, so having more arboreal elements of different types and arrangements within pastures would increase species richness. On the other hand, the spatial variation of the basal area of woody vegetation was poorly explained by our models.

We determined that the combination of high resolution aerial photographs and vegetation height information derived from DEM data is a powerful approach for quantitatively assessing landscape heterogeneity (i.e., the presence and proportion of different land cover types

within a landscape) in fragmented landscapes. This structural landscape heterogeneity was strongly and positively related to heterogeneity in floristic composition. Sampling plots with a high proportion of forest cover and heterogeneity in woody cover classes not only had high species richness within the plot, but had notably higher variability in floristic composition among plots than sites that had a simpler structure. Our analysis, by distinguishing the different types of forest cover classes, showed that the greatest contribution to woody species richness and heterogeneity within plots is made by two main types of arboreal cover: forest fragments with a tall canopy and isolated trees. The contribution of the former to richness is almost self-explanatory since they contain the highest species density and diversity of woody plants in the landscape, so if the plot sampled included even a small portion of one of these fragments, its contribution to richness was great. However, while the contribution of isolated trees to richness and floristic heterogeneity is good news, it is not as obvious; their diversity and density reflect complex management decisions by each farmer, and therefore varies widely among pastures. Our results demonstrate that isolated trees are important to maintain the species richness and floristic heterogeneity of woody plants in rural landscapes dedicated to cattle raising.

Isolated trees scattered in pastures have an enormous potential for catalyzing and accelerating secondary succession in fragmented landscapes by acting as regeneration nuclei (Guevara et al., 2005), and they may also be important seed sources (Laborde et al., 2008). A relatively high density and diversity of isolated trees within pastures could be one of the reasons why proximity to forest fragments or to forested riparian belts was not related to woody species richness in our plots. Additionally, several authors have proposed that isolated trees may form part of complex, structured matrices, which enhance and maintain the availability of different resources within pastures and crop-fields (Fahrig et al., 2011; Guevara et al., 1998; Harvey et al., 2011). A relatively high density and diversity of isolated trees increase landscape connectivity and represent a ubiquitous device that can enhance resilience in agricultural landscapes. These trees, properly managed, could play an important role as landscape keystone structures for the conservation of native biodiversity and the provision of ecosystem services (Guevara et al., 2005; Manning et al., 2006).

Pastures that have very low woody cover, similar to our sampled plots of scenarios I and II ($\leq 15\%$), should be targeted to increase the proportion of woody cover that they have, in order to increase the abundance and richness of woody species. A more specific and optimal goal would be to reach between 20 and 40% of woody cover in all pastures (resembling our scenarios III and IV), by increasing the density of isolated trees in open pastures and also by promoting passive or active restoration of woody vegetation in small patches scattered throughout those areas. These should be incentivized with schemes similar to those used in the payment of environmental services in order to increase the conservation potential and resilience of this rural landscape. Structural landscape metrics, incorporating high resolution image analysis and height data information (i.e., LIDAR-DEM data), could be used to detect which farmers attain these goals and have arboreal or forested patches with trees > 10 m tall since they are the landscape elements that contribute the most to conservation and connectivity.

5. Conclusions

It is clear that more complex and heterogeneous agricultural matrices could retain and enhance woody plant diversity, while maintaining several ecosystem functions. We highlight how, of the landscape composition metrics used, forest cover is the strongest indicator of woody vegetation richness and abundance, while landscape heterogeneity is strongly associated with high floristic heterogeneity. As we show in this study, the combination of high resolution images with vegetation height data, obtained from remote sensing, is a powerful tool for the assessment of landscape heterogeneity. Forest fragments with

relatively tall canopies (> 10 m) and isolated pasture trees are crucial for the conservation of native forest flora. Based on our findings, we propose that strategies aimed at increasing the area of woody cover and diversity of woody plants within pastures be implemented to maximize the heterogeneity of arboreal or forested elements within the agricultural landscape. This will promote the conservation of biodiversity, and will enhance forest resilience and the sustainability of tropical landscapes dedicated to raising livestock. This is a concrete proposal that should be made to farmers in rural landscapes and is particularly crucial in highly deforested landscapes such as those of central Veracruz, and the entire lowland tropical region of Mexico and Central America; even more so given the current and troubling future scenario of global climate change in the region.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2019.01.072>.

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