Effects of Spatial Patch Characteristics and Landscape Context on Plant Phylogenetic Diversity in a Naturally Fragmented Forest

Authors: Arellano-Rivas, Amaranta, Munguía-Rosas, Miguel A., De-Nova, J. Arturo, and Montiel, Salvador

Effects of Spatial Patch Characteristics and Landscape Context on Plant Phylogenetic Diversity in a Naturally Fragmented Forest

Amaranta Arellano-Rivas[1,2], Miguel A. Munguía-Rosas[2], J. Arturo De-Nova[1,3], and Salvador Montiel[2]

Abstract

Phylogenetic diversity is a reliable predictor of taxonomic and functional diversity and of biodiversity option value. During forest fragmentation, forest patches that vary in size, degree of isolation, and shape are formed. Identifying the spatial characteristics of forest remnants that maximize phylogenetic diversity could be useful to conservationists when prioritizing areas to be protected if resources are limited. In this study, we assessed whether spatial patch characteristics (size, edge density, and shape) and the context of the patch in the surrounding landscape (i.e., isolation degree) affect plant phylogenetic diversity in 19 naturally shaped forest patches. Owing to the age of the forest patches, the study system allowed us to assess the long-term effects of spatial variables on phylogenetic diversity. We found that patch size has a positive effect on phylogenetic diversity, presumably because environmental heterogeneity and niche opportunities are greater in bigger patches. Also, phylogenetic diversity was positively affected by edge density. The convergent evolution of traits which confer tolerance to prevailing edge conditions in phylogenetically distant species may explain this result. We suggest that patch size is a reliable predictor of plant phylogenetic diversity and could be used as a prioritization criterion in conservation strategies, at least in the study area.

Introduction

Biodiversity conservation is particularly urgent in the tropics where a highly diverse biota exists in the context of massive rates of habitat loss (Achard et al., 2002). The assessment of biodiversity and how human-driven disturbances affect it have mostly focused on taxonomic diversity (e.g., species richness; Fahrig, 2003). However, taxonomic diversity assumes that species are homogeneous entities and neglects the evolutionary history of species. Phylogenetic diversity, understood as the evolutionary history contained in a biotic community (Faith, 1992), may be a more informative metric of biodiversity because it is a reliable predictor of the main ecological processes that structure biotic communities (Cadotte, Cardinale, & Oakley, 2008; Faith et al., 2010; Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011), and of biodiversity option value (Faith et al., 2010). Phylogenetic diversity may also provide a useful tool

for conservationists; for example, it may help identify land areas with a longer evolutionary history, those with the most prolific lineages or the taxa most prone to extinction (Brooks, Mayden, & McLennan, 1992; Faith, 1992; Faith et al., 2010). Despite the relevance phylogenetic diversity may have in fundamental and applied fields of ecology, it was not until recently that ecologists started looking at the effects of human-driven

[1]Instituto de Investigación de Zonas Desérticas, Universidad Autónoma de San Luís Potosí, México
[2]Departamento de Ecología Humana, Centro de Investigación y Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México
[3]Facultad de Agronomía, Universidad Autónoma de San Luís Potosí, México

Corresponding Author:
Miguel A. Munguía-Rosas, Laboratorio de Ecología Terrestre, Cinvestav-Mérida, KM 6 Antigua carretera a Progreso, C.P. 97203 Mérida, México.
Email: munguiarma@cinvestav.mx

disturbance on phylogenetic diversity (e.g., Ribeiro et al., 2016). Some studies have tested the prediction that anthropogenic disturbance (e.g., agriculture [Dinnage, 2009], chronic human disturbance [Ribeiro et al., 2016], and logging [Tamoya et al., 2015]) impoverish plant phylogenetic diversity, the underlying mechanism being identified as the phylogenetic conservation of functional traits associated with the vulnerability of plants to disturbance (e.g., shade tolerance, large seeds, and hard wood; Laurance et al., 2006; Lopes, Girão, Santos, Peres, & Tabarelli, 2009; Silva & Tabarelli, 2000). As a result, plant communities in more disturbed habitats are expected to be more phylogenetically related, a prediction frequently supported by data (Egorov et al., 2015; Ribeiro et al., 2016; Tamoya et al., 2015).

A major threat to biodiversity is habitat loss and fragmentation, a process that encompasses several changes in the spatial characteristics and configuration of habitat remnants at the patch and landscape levels (Fahrig, 2003). Although several studies have shown that habitat loss at the patch level has a particularly strong negative effect on taxonomic diversity (Bender, Contreras, & Fahrig, 1998; Mazerolle & Villard, 1999; Valdés et al., 2015), the few studies available have not found any effect of patch size, isolation, or shape on phylogenetic diversity in tropical plant communities (Arroyo-Rodríguez et al., 2012; Santos, Arroyo-Rodríguez, Moreno, & Tabarelli, 2010). Instead, previous studies have found that phylogenetic diversity is influenced by the age of forest patches (Santos et al., 2010, 2014), suggesting that elapsed time since the fragmentation process began (from decades to just a few hundred years) was possibly not long enough to reveal any effect on phylogenetic diversity (Santos et al., 2010, 2014). Therefore, forest which has been fragmented for longer periods of time, such as naturally fragmented forests, are ideal model systems for assessing the long-term effects of spatial variables on phylogenetic diversity (Munguía-Rosas et al., 2014). This information may both improve our understanding of how spatial patch variables affect phylogenetic diversity and help identify which spatial attributes of habitat remnants would maximize the long-term conservation of phylogenetic diversity.

In this study, we evaluated whether the spatial characteristics of forest patches (size, shape, and edge density) and their context in the landscape (distance to the continuous forest and distance to the nearest patch) predict plant phylogenetic diversity in a naturally fragmented tropical forest of the Yucatan. This forest is composed of natural vegetation patches that vary naturally in size, degree of isolation, and shape (Mas & Correa, 2000; Munguía-Rosas & Montiel, 2014). These forest patches are discrete units with clearly identifiable edges (Durán, 1987; Rico-Gray, 1982). The vegetation of these patches is richer in species and structurally more complex than

that of the habitat matrix, which is dominated by flood-tolerant species (Rico-Gray & Palacios-Rios, 1996). Because this forest has been fragmented for over a million years (CONANP-SEMARNAT, 2006), it offers an excellent opportunity to study the long-term effects of spatial patch variables on phylogenetic diversity (Montiel, Estrada, & León 2006; Munguía-Rosas & Montiel, 2014).

Patch area is positively related to environmental heterogeneity, and smaller patches may represent a more restricted niche for a reduced number of potentially more closely related species (Arellano-Rivas, De-Nova, & Munguía-Rosas, 2017). Also, patch isolation may filter plant species that have a long-distance dispersal capacity, such as plants with zoochory, a phylogenetically conserved trait (Rezende, Lavabre, Guimarães, Jordano, & Bascompte, 2007). Moreover, the amount of edge of a patch increases with shape complexity, and edges have harsher environmental conditions (Murcia, 1995) where mostly pioneer-like, closely related plant species can survive (Letcher, 2010; Tabarelli, Lopes, & Peres, 2009). And finally, because of the chronic flooding that prevails in the habitat matrix, patches with a lower elevation are at a higher risk of flooding; thus, a larger proportion of flood-tolerant plants (a phylogenetically conserved trait [Tanentzap & Lee, 2017]) is expected in these patches. It is not unreasonable to expect that plant communities in habitat patches with spatial variables associated with harsher environmental conditions (reduced area, high isolation degree, convoluted shape, and low elevation) would have lower phylogenetic diversity.

Methods

Study Area

The study area was the Petenes-Celestún-El Palmar Biological Corridor (19° 53′–21° 11′ N, 90° 28′–90° 17′ W), located along the northwestern coast of the Yucatan Peninsula (Figure 1). The climate is tropical subhumid with summer rains. Precipitation ranges from 1,000 to 1,200 mm y^{-1} and temperature from 26.1°C to 27.8°C (Durán, 1987). The study was conducted on patches of semievergreen tropical forest locally known as *petenes* (singular: *peten*; Figure 1). These forest patches are surrounded by a flooded matrix of shorter, less diverse vegetation that is tolerant to flooding and dominated by sedges and short mangroves (Rico-Gray, 1982; Rico-Gray & Palacios-Rios, 1996). The forest becomes continuous as one moves inland. In our sample, patch size ranges from 1.6 to 320 ha, and shape index (SI) is 0.26 to 1.62. The distance to the nearest patch and distance to the continuous forest are 0.03 to 1.62 km and 4 to 9 km, respectively. Most forest patches have a constant fresh water supply from sinkholes and are located at a relatively higher elevation; two characteristics that may
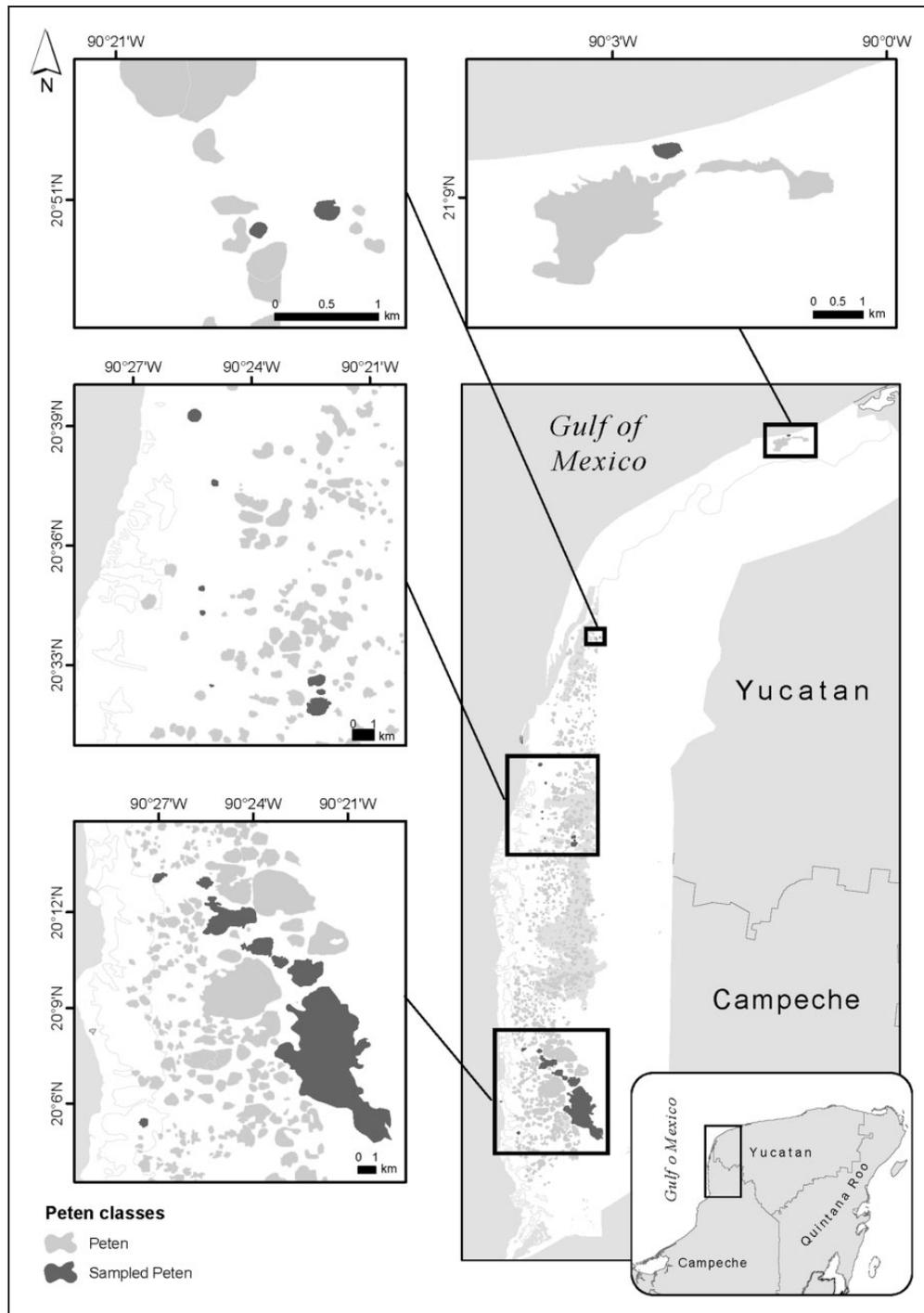
Figure 1. Map of the study area (Petenes-Celestún-El Palmar Biological Corridor, polygon in white). Forest patches sampled (Sampled peten) are shown in black. Patches not sampled are in gray (peten). The small rectangle in the insert at the bottom right indicates the position of the study area on the Yucatan Peninsula. All bars represent 1 km.

at least partially explain the presence of these forest patches in the study area (Barrera, 1982; Rico-Gray, 1982). The forest patches grow on quaternary geological formations that are about 1.7 Ma old (CONANP-SEMARNAT, 2006).

Dominant canopy species are *Annona glabra*, three species of *Ficus*, *Laguncularia racemosa*, *Manilkara zapota*, *Metopium brownei*, *Swietenia macrophylla*, and *Tabebuia rosea*. In the understory, dominant species are as follows: *Acrostichum aureum*, *Bravaisia tubiflora*, and

Sabal yapa. The herbaceous layer is scarce or absent. Dominant species in the matrix are *Acrostichum danaeifolium*, *Cladium mariscus*, *Avicennia germinans*, *L. racemosa*, and *Rhizophora mangle* (Durán, 1995; Rico-Gray, 1982).

Plant Sampling

Due to insurmountable problems with accessibility, a non-random sample of 19 forest patches that were accessible and had an area greater than 1 ha was chosen (Figure 1). From January 2013 to August 2014, we recorded the vascular plant species in these patches using a sampling protocol modified from Gentry (1982). In short, plant sampling was conducted using 54×4 m belt transects. Five transects were set up in each patch, the first transect was placed using a random GPS point previously located on digital cartography, and the remaining transects were systematically placed parallel to the first and 20 m apart. Total sampled area per patch was 0.1 ha. Based on experience gleaned from previous studies (Arroyo-Rodríguez et al., 2012; Arroyo-Rodríguez, Pineda, Escobar, & Benítez-Malvido, 2009; Munguía-Rosas & Montiel, 2014; Rosati, Fipaldini, Marignani, & Blasi, 2010), the area sampled was kept constant across patches to reduce sample area effects. Only plants with a girth greater than 5 cm (dbh $= 1.6$ cm), and nonwoody plants taller than 20 cm were sampled. Epiphytes and lianas were not recorded during the vegetation survey owing to the difficulties associated with assessing their presence and abundance. Plants were identified with the help of field guides (Brokaw et al., 2011; Pennington & Sarukhán, 2005) and expert advice. To assess sampling completeness, we plotted species accumulation curves and compared observed species richness with that predicted by nonparametric estimators (Chao1, Chao2, and Abundance-based Coverage Estimator [ACE]).

Spatial Variables of Forest Patches

The most recent digital cartography (2009 and 2011) available for the study area in Google Earth Pro 7.2 was used to calculate patch size (measured in hectares), and distance to the continuous forest (edge-to-edge in kilometers), distance (edge to edge) to the nearest patch (km), edge density (patch perimeter [m]/patch size [ha]), patch elevation at its center (m a.s.l.) were calculated using ArcInfo 9.2. Some of this information was used to calculate a SI as follows: $SI = \frac{p}{2\sqrt{\pi S}}$ where p is the perimeter of the focal patch (m), and S is the size (ha) of the focal patch. This index describes the complexity of patch shape relative to a perfectly circular shape. *SI* is equal to 1 if the patch is nearly circular and increases with patch shape complexity (convoluted shape). Some spatial data (patch elevation and distance to the nearest patch) were

validated in the field using a GPS for some patches (4), confirming that the data obtained from digital cartography were accurate. According to suppliers, the images used to calculate spatial variables were taken during the dry season, when there is less cloud cover.

Phylogeny and Phylogenetic Diversity Metrics

A preliminary phylogeny of the 47 plant species was built by matching the list of species obtained from our vegetation survey with up-to-date family and genus names, and tip labels of a megatree (Webb, Ackerly, & Kembel, 2008), using the dated phylogenetic hypothesis from Davies et al. (2004) and Magallón, Gómez-Acevedo, Sánchez-Reyes, & Hernández-Hernández (2015) for seed plants. These megatrees are robust and were built with sequences of plastid and nuclear genetic markers to estimate the relative timing of branching events, and they are calibrated with the fossil records (Davies et al., 2004; Magallón et al., 2015). This preliminary phylogeny was built with the help of PHYLOMATIC function of PHYLOCOM 4.2 (Webb et al., 2008). The ultrametric phylogeny with branch lengths in millions of years was obtained using the bladj option in PHYLOCOM. This function fixes the ages of the root node and other nodes based on Wikström, Savolainen, and Chase (2001). Because this phylogeny had some polytomies that could affect the accuracy of phylogenetic diversity metrics (Swenson, 2009), we fully resolved within-family species relationships by manually incorporating the available information (topology and branch length) in molecular phylogenies at the family level for Leguminosae (LPWG, 2013), Myrtales (Berger, Kriebel, Spalink, & Sytsma, 2016), Sapindales (Buerki et al., 2010; Muellner-Riehl et al., 2016), and the genus *Ficus* (Cardoso-Pederneiras, Romaniuc-Neto, & de-Freitas-Mansano, 2015; Chantarasuwan, Rønsted, Kjellberg, Sungkaew, & van Welzen, 2016; Ibarra-Manríquez, Cornejo-Tenorio, González-Castañeda, Piedra-Malagon, & Luna, 2012).

Two fern species found in the communities sampled were excluded, as recommended by other authors (Arroyo-Rodríguez et al., 2012; Honorio-Coronado et al., 2015) because they would have contributed disproportionately to phylogenetic diversity metrics owing to their low degree of relatedness to the majority of the other species. Trees were visualized and exported using FigTree v.1.4.2. The final phylogenetic tree used for calculating phylogenetic diversity metrics is shown in Figure 2.

The time-calibrated phylogenetic tree was used to calculate abundance-weighted metrics of phylogenetic diversity per forest patch. We calculated the standardized effect size of phylogenetic diversity *sensu stricto* (hereafter ses PD). This metric represents the deviation, in branch length, of the phylogeny of all species occurring in a given
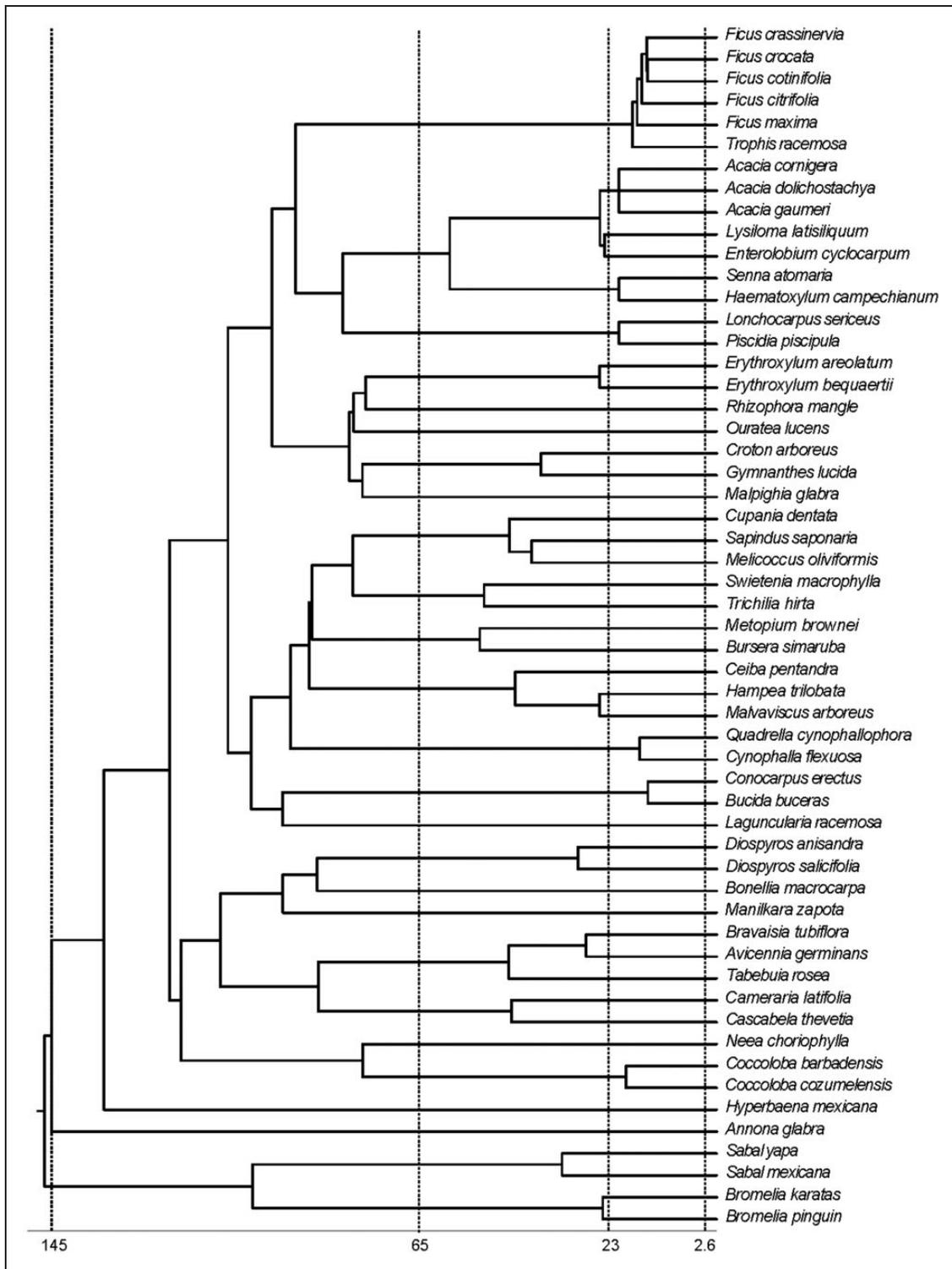
Figure 2. Phylogenetic relationships of 47 plant species recorded during a vegetation survey in 19 forest patches of the Yucatan. Phylogenetic relationships of species were fully resolved; divergence times were very short for *Ficus* and *Acacia* species. Numbers at the bottom are divergence times (millions of years).

patch (Faith, 1992), from branch length obtained from random shuffling phylogeny tips 999 times (Swenson, 2014). This deviation was standardized and then expressed in standard deviations using the following equation: $ses\ PD = (PD_s - PD_r)/\sigma_r$, where PD_s is the total branch length in a given patch, PD_r is the branch length obtained from randomizations, and σ_r is the standard deviation from the randomized set (Webb, Ackerly, McPeek, & Donoghe, 2002). The mean pairwise phylogenetic distance (MPD) and the mean pairwise distance to the nearest taxon (MNTD) between species in the phylogeny were also calculated. Finally, we calculated the inverse of the standardized effect sizes of MPD and MNTD, better known as net relatedness index (NRI) and nearest taxon index (NTI; Webb, 2000; Webb et al., 2002). NTI and NRI are calculated in an analogous manner, using the following expression: $NTI/NRI = -1\ (N_s - N_r)/\sigma_r$, where N_s is the average (NRI) or average nearest taxon (NTI) distance in a given patch, N_r is the average nearest taxon distance obtained from a set of randomized samples (999 permutations), and σ_r is the standard deviation from the randomized set (Webb, 2000; Webb et al., 2002). MPD and MNTD are metrics of phylogenetic diversity at the basal and terminal levels and are measured in millions of years (Swenson, 2014; Webb et al., 2002); these metrics along with ses PD will be referred to hereafter as metrics of phylogenetic diversity. NRI and NTI are metrics of phylogenetic structure (Kembel et al., 2010; Webb et al., 2002), with positive values representing basal and terminal familial phylogenetic clustering, respectively, while negative values suggest phylogenetic overdispersion (Webb et al., 2002). We preferred to use ses PD instead of total branch length of the phylogeny of the community (i.e., faiths' phylogenetic diversity metric) because the latter is typically strongly correlated with species richness (for our data set: $r = 0.98$, $p \ll .01$), and ses PD fixes this issue (Honorio-Coronado et al., 2015; Swenson, 2014; ses PD vs. species richness $r = -0.083$, $p \gg .05$). All the metrics were calculated using the PICANTE library (Kembel et al., 2010) for R 3.2 software (R Development Core Team, 2015).

Statistical Analysis

To assess the relationship between metrics of phylogenetic diversity and phylogenetic structure with spatial patch variables, we used multiple regression models. In the models, ses PD, MPD, MNTD, NRI, and NTI were the response variables (a different model per metric), and the spatial variables of patches (patch size, distance to continuous forest, distance to the nearest patch, edge density, central patch elevation, and patch SI) were the explanatory variables. To improve linearity, patch size, distance to the nearest patch, and distance to the

continuous forest were log transformed. Multicollinearity among the response variables was assessed with the variance inflation factor, which was <4 in all cases (variance inflation factor = 1.9–3.9) suggesting a low degree of multicollinearity. An assessment of statistical power (β) suggests that it is within the optimal range (β = 0.81–0.93) for most metrics (MPD, MNTD, NTI, and NRI) and very close to the optimal for ses PD (β = 0.73).

All of the statistical analyses were run in R 3.2 (R Development Core Team, 2015).

Results

Species Richness and Major Clades

Forty-seven plant species were recorded in the 19 forest patches we sampled, these species belong to 25 plant families. An a *posteriori* evaluation provided evidence that sampling was representative in all these patches (i.e., the species accumulation curves reached an asymptote, and species representativeness was greater than 80% in all patches). Mean number of species per family was 1.88 ± 0.28 (hereafter mean values ± 1 *SE*), and the most speciose families were Moraceae (7) and Fabaceae (5; range 1–7 species per family). The patches had mainly eudicots and a just a few species of magnolids (only one species in some patches) and monocots (only 1–2 species in some patches). Species richness per patch ranged from 5 to 20 species, and the number of families per patch ranged from 5 to 17.

Relationship of Spatial Patch Variables With Phylogenetic Diversity

Ses PD, NRI, and NTI were significantly affected by edge density, and the direction of this effect was positive for ses PD and negative for NRI and NTI. Edge density explained more than 30% of the variance in ses PD and NTI, and about 17% of the variance in NRI. Patch size had a significant and positive effect on MNTD and a negative effect on NRI and NTI. Patch size explained 18%, 47%, and 13% of the variation in MNTD, NRI, and NTI, respectively. The other explanatory variables included in the models were not statistically significant predictors of ses PD, MNT, NRI, or NTI. No explanatory variable included in the regression model significantly affected MPD. The proportion of explained variance (R^2) of the full models ranges from 0.48 to 0.76 (Table 1).

Discussion

In this study, we assessed whether spatial characteristics and context in the landscape surrounding forest patches

Table 1. Results of Multiple Linear Regression Models to Assess the Effects of Spatial Patch Variables (Patch Size [Size], Distance to the Continuous Forest [D Continuous F], Distance to the Nearest Patch [D Nearest], Patch Elevation [Elevation], Patch Shape [Shape], and Edge Density [Edge D]) on Phylogenetic Diversity Metrics (Standardized Phylogenetic Diversity Effect Size [ses PD], Mean Pairwise Distance [MPD], Mean Pairwise Distance to the Nearest Taxon [MNTD], Net Relatedness Index [NRI], and Nearest Taxon Index [NTI]).

Response	Source of variation	Statistic	Coefficient ($\pm 1SE$)	Explained variance (%)	R^2
Ses PD	Size	0.08	0.91 ± 0.36	0.32	0.48
	D Continuous F	1.57	-0.07 ± 0.21	6.77	
	D Nearest	0.22	0.08 ± 0.15	0.97	
	Elevation	0.06	-0.01 ± 0.04	0.24	
	Shape	0.24	-2.51 ± 1.51	1.06	
	Edge D	9.09*	15.26 ± 5.06*	39.05	
MPD	Size	2.51	14.09 ± 14.57	9.15	0.56
	D Continuous F	0.61	10.41 ± 8.55	2.24	
	D Nearest	0.54	5.35 ± 6.11	1.98	
	Elevation	3.09	-0.95 ± 1.75	11.25	
	Shape	4.11	2.69 ± 60.13	14.94	
	Edge D	4.58	433.97 ± 202.76	16.69	
MNTD	Size	4.86*	33.34 ± 26.14*	18.27	0.55
	D Continuous F	0.38	13.91 ± 15.34	1.42	
	D Nearest	0.08	2.35 ± 10.96	0.29	
	Elevation	4.73	5.23 ± 3.15	17.77	
	Shape	0.63	-134.95 ± 107.85	0.23	
	Edge D	4.52	772.88 ± 363.64	16.95	
NRI	Size	21.56**	-0.83 ± 0.38*	47.43	0.76
	D Continuous F	0.09	-0.16 ± 0.19	0.19	
	D Nearest	0.14	-0.02 ± 0.14	0.28	
	Elevation	2.12	0.12 ± 0.40	4.21	
	Shape	4.43	5.17 ± 2.36	7.13	
	Edge D	5.97*	-11.24 ± 4.59*	16.83	
NTI	Size	5.04*	-1.04 ± 0.46*	13.44	0.64
	D Continuous F	1.35	-0.56 ± 0.27	3.99	
	D Nearest	0.68	0.11 ± 0.19	2.04	
	Elevation	4.53	-0.08 ± 0.05	14.39	
	Shape	0.01	4.11 ± 1.93	0.01	
	Edge D	10.18*	-20.82 ± 6.53*	30.12	

All statistics are F values with 6 and 12 degrees of freedom. Per-term coefficient and explained variance as well as the R^2 of the full model proposed per response variable are also shown. Patch size, distance to the continuous forest, and distance to the nearest patch were log-transformed to improve linearity.
*$p < .05$. **$p < .01$.

are reliable predictors of phylogenetic diversity and structure. This is important because if spatial patch variables predict these components of phylogenetic diversity, the former could be used as a prioritization criterion for forest remnants in conservation efforts when resources are limited. Owing to the longevity of some tropical plants, it is important to control for the age of forest patches because of the risk of underestimating an effect on PD in recently shaped patches (Munguía-Rosas et al.,

2014). Therefore, we used as a study model a naturally fragmented forest where the forest patches are more than a million years old (CONANP-SEMARNAT, 2006). According to the results, some spatial variables at the patch level are reliable predictors of phylogenetic diversity and structure. As expected, plant communities of larger forest patches are more phylogenetically diverse and overdispersed. We suggest that greater environmental heterogeneity and wider niche opportunities may

favor the co-occurrence of distantly related species in the larger patches. Surprisingly, patches with larger edge density are phylogenetically more diverse and overdispersed than the expected by chance. Plant traits that confer a tolerance to the environmental conditions that prevail in the edges are not likely to be phylogenetically conserved but rather, in this study system in particular, these traits may have evolved in distantly related plants. Thus, we suggest that larger patches are important reservoirs of phylogenetic diversity, and patch size may be a useful proxy for phylogenetic diversity and structure and could be used as a prioritization criterion for conservation purposes.

Patch size has long been identified as a reliable predictor of taxonomic diversity in forests fragments (e.g., Bender et al., 1998; Munguía-Rosas & Montiel, 2014). However, its relevance in predicting other major components of biodiversity, such as phylogenetic diversity, has been poorly documented, and the few available studies have found no significant effect (Arroyo-Rodríguez et al., 2012; Santos et al., 2010). In contrast to previous studies, we found that patch size is a reliable predictor of phylogenetic diversity at the terminal level and of phylogenetic structure. Phylogenetic diversity and overdispersion increase with the size of patches. The association between these variables may be due to the frequent positive association between habitat size and environmental heterogeneity (e.g., Kadmon & Allouche, 2007), which promotes niche partitioning and functional diversification (Bergholz et al., 2017), with the latter often positively correlated with phylogenetic diversity and structure (Cavender-Bares, Kozak, Fine, & Kembel, 2009; but see Xu et al., 2016). On the other hand, we also found that phylogenetic diversity (ses PD) and overdispersion at the terminal (NTI) and familial (NRI) levels increasingly deviated from what would be expected by chance as edge density increases. This is a surprising result because it implies that patches with a larger proportion of edge are more phylogenetically diverse, contrary to our expectation. We predicted that harsher environmental conditions associated with patch edges would promote the proliferation of disturbance-tolerant, often closely related plant species, as evidenced by previous studies in anthropogenic forest fragments (Laurance & Yensen, 1991; Mo, Shi, Zhang, Zhu, & Slik, 2013; Santos et al., 2010). However, when the functional traits that favor the permanence or proliferation of plants in the forest edges are present in phylogenetically distant lineages, phylogenetic diversity can increase with the amount of edge. In the study area, environmental filters such as flooding and salinity have a relatively larger influence on plants occurring in the edges of forest patches (Rico-Gray & Palacios-Rios, 1996). In contrast to other plant communities exposed to chronic flooding (Tanentzap & Lee, 2017), in the study area, traits associated with tolerance to flooding are ecological convergences present in phylogenetically distant plant species. An illustrative example are the mangrove species *R. mangle* (Rhizophoraceae), *A. germinans* (Acanthaceae), and *L. racemosa* (Combretaceae) that are tolerant to flooding and salinity, abundant in the edges of patches in the study area, and phylogenetically distant.

Spatial variables such as patch shape and elevation did not affect phylogenetic diversity or structure. We think this was due to the narrow range of variation in these variables. Patch elevation ranges from 3 to 8 m a.s.l., within which any important variation in plant species composition is unlikely. Similarly, variation in SI was minimal (0.26–1.62). Although patches were fairly isolated in the study area (distance to the continuous forest is 4–9 km), the lack of an effect of this variable on phylogenetic diversity and structure may be due to the fact that long-distance seed dispersal (animal- and water assisted) is a widespread trait among plant species in the study area (personal observation of the authors), and the habitat matrix does not represent a barrier for seed vectors. Finally, though the statistical power of our analysis was acceptable for most of the metrics, statistical power for ses PD was slightly lower than optimal ($\beta = 0.7$); thus, an increase in sample size could increase the chance of finding a significant effect of the predictors on this metric.

Previous studies have found no effect of spatial patch variables on phylogenetic diversity or structure in recent (from decades or just a few hundred years) and anthropogenically shaped patches of tropical forest (Arroyo-Rodríguez et al., 2012; Santos et al., 2010, 2014). In contrast, we found an effect of patch size and edge density. The lack of an effect in previous studies could be due to the young age of patches. Owing to the great longevity of some plants (especially trees), more than a century may pass before local extinction could be detected in forest plants (Vellend et al., 2006). This notion is also supported by the fact that some of the previous studies have detected an effect of patch age on phylogenetic diversity (Santos et al., 2010, 2014). It is known that forest fragmentation is actually a series of processes during which the spatial patch variables evaluated in this study represent only a subset of the modifications that may occur during forest fragmentation (Fahrig, 2003; Hadley & Betts, 2016). Habitat loss often has a stronger effect on taxonomic diversity at the patch level than at the landscape level (Fahrig, 2003). However, in the study area, we detected a significant effect of habitat loss on phylogenetic diversity at both the patch (this study) and the landscape levels (Munguía-Rosas et al., 2014), in contrast with the findings of previous studies which found no effect of habitat loss on phylogenetic diversity at the patch or landscape level (Arroyo-Rodríguez et al., 2012; Santos

et al., 2010). Potentially, these contrasting results may result from differences in elapsed time since fragmentation began. However, differences in the origin of fragmentation (natural vs. anthropogenic) and the type of matrix could explain among study differences in the results.

In conclusion, patch size is a reliable predictor of phylogenetic diversity and structure, and we suggest that the underlying mechanism is that larger patches also offer greater environmental heterogeneity and niche opportunities. The observed positive effect of edge density on phylogenetic diversity and structure seems to be due to the ecological convergence in distantly related species of plant traits associated with tolerance to flooding, which is a prevalent condition in the edges of forest patches in the study area.

Implications for Conservation

In recent years, conservationists have turned to phylogenetic diversity owing to its positive correlation with ecosystem processes, environmental services, and biodiversity option value (Faith et al., 2010). Therefore, the identification of a/some spatial variable(s) that are correlated with phylogenetic diversity would be helpful to identify forest remnants that are relevant to conservation. Our results suggest that patch size may be a reliable predictor of phylogenetic diversity and could be used as a prioritization criterion in conservation strategies, at least in the study area.

References

Achard, F., Eva, H. D., Stibing, H.-J., Mayaux, P., Gallego, J., Richards, T., & Malingreau, J.-P. (2002). Determination of deforestation rate of the world's humid tropical forests. *Science*, *297*, 999–1002.

Arellano-Rivas, A., De-Nova, A., & Munguía-Rosas, M. A. (2017). Patch isolation and shape predict plant functional diversity in a naturally fragmented forest. *Journal of Plant Ecology*, *10*, ▮▮ doi:10.1093/jpe/rtw119.

Arroyo-Rodríguez, V., Cabender-Bares, J., Escobar, F., Melo, F. P. L., Tabarelli, M., & Santos, B. A. (2012). Maintenance of tree phylogenetic diversity in highly fragmented rain forest. *Journal of Ecology*, *100*, 702–711.

Arroyo-Rodríguez, V., Pineda, E., Escobar, F., & Benítez-Malvido, J. (2009). Value of small patches in the conservation of plant-species diversity in highly fragmented rain forest. *Conservation Biology*, *23*, 729–739.

Barrera, A. (1982). Los petenes del noroeste de Yucatán: su exploración ecológica en perspectiva [The petenes of northwestern Yucatan: Ecological exploration and perspectives]. *Biótica*, *2*, 163–169.

Bender, D. J., Contreras, T. A., & Fahrig, L. (1998). Habitat loss and population decline: A meta-analysis of the patch size effect. *Ecology*, *79*, 517–533.

Berger, A. B., Kriebel, R., Spalink, D., & Sytsma, K. J. (2016). Divergence times, historical biogeography, and shifts in speciation rates of Myrtales. *Molecular Phylogenetics and Evolution*, *95*, 116–136.

Bergholz, K., May, F., Giladi, I., Ristow, M., Ziv, Y., & Jeltsh, F. (2017). Environmental heterogeneity drives fine-scale species assembly and functional diversity of annual plants in a semi-arid environment. *Perspectives in Plant Ecology, Evolution and Systematics*, *24*, 138–143.

Brokaw, N., Bonilla, N., Knapp, S., MacVean, A., Ortíz, J. J., Peña-Chocarro, M., . . . Tun-Garrido, J. (2011). *Arboles del mundo maya [Trees of the Maya World]*. Mérida, México: Natural History Museum, Pronatura, UADY, UVG.

Brooks, D. R., Mayden, R. L., & McLennan, D. A. (1992). Phylogeny and biodiversity: Conserving our evolutionary legacy. *Trends in Ecology and Evolution*, *7*, 55–59.

Buerki, S., Lowry, P. P., Alvarez, N., Razafimandimbison, S. G., Kuüpfer, P., & Callmander, M. W. (2010). Phylogeny and circumscription of Sapindaceae revisited: Molecular sequence data, morphology and biogeography support recognition of a new family, Xanthoceraceae. *Plant Ecology and Evolution*, *143*, 148–159.

Cadotte, M. W., Cardinale, B. J., & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of National Academy of Sciences of United States of America*, *105*, 17012–17017.

Cardoso-Pederneiras, L., Romaniuc-Neto, S., & de-Freitas-Mansano, V. (2015). Molecular phylogenetics of Ficus section pharmacosycea and the description of Ficus subsection Carautaea (Moraceae). *Systematic Botany*, *40*, 504–509.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*, 693–715.

Chantarasuwan, B., Rønsted, N., Kjellberg, F., Sungkaew, S., & van Welzen, P. C. (2016). Palaeotropical intercontinental disjunctions revisited using a dated phylogenetic hypothesis with nearly complete species level sampling of *Ficus* subsect. Urostigma *(Moraceae)*. Journal of Biogeography, *43*, 384–397.

CONANP-SEMARNAT (2006) *Programa de conservación y manejo de la Reserva de la Biosfera Los Petenes* [Conservation and management program of the Petenes Biosphere Reserve].

Mexico City, Mexico: CONANP. Retrieved from http://www.co-nanp.gob.mx/anp/consulta/PCM-petenes.pdf.

Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E., & Savolainen, V. (2004). Darwin's abominable mystery: Insights from a supertree of the angiosperms. *Proceedings of National Academy of Sciences of the United States of America*, *101*, 1904–1909.

Dinnage, R. (2009). Disturbance alters the phylogenetic composition and structure of plant communities in an old field system. *PLoS One*, *4*, e7071.

Durán, R. (1987). Descripción y análisis de la estructura y composición de la vegetación de los petenes del noroeste de Campeche, México [Description and analysis of the vegetation structure and composition of the petenes in northeastern Campeche, Mexico]. *Biótica*, *12*, 191–198.

Durán, R. (1995). Diversidad florística de los petenes de Campeche [Flora of the Petenes of Campeche]. *Acta Botánica Mexicana*, *31*, 73–84.

Egorov, E., Prati, D., Durka, W., Michalski, S., Fischer, M., Schmitt, B., . . . Brändle, M. (2015). Does land-use intensification decrease plant phylogenetic diversity in local grasslands? *PLoS One*, *9*, e103–e252.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, *34*, 487–515.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*, 1–10.

Faith, D. P., Magallón, S., Hendry, A. P., Conti, E., Yahara, T., & Donoghue, M. J. (2010). Ecosystem services: An evolutionary perspective on the links between biodiversity and human well-being. *Current Opinion in Environmental Sustainability*, *2*, 1–9.

Flynn, D. F., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity—Ecosystem-function relationships. *Ecology*, *92*, 1573–1581.

Gentry, A. H. (1982). Patterns of neotropical plant species diversity. In: M. K. Hetch, R. J. MacIntyre, & M. T. Clegg (Eds.). *Evolutionary biology* (Vol. 15, (pp. 1–85). New York, NY: Springer.

Hadley, A. S., & Betts, M. G. (2016). Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports*, *1*, 1–12.

Honorio-Coronado, E. N., Dexter, K. G., Pennington, R. T., Chave, J., Lewis, S. L., Alexiades, M. N., . . . Phillips, O. L. (2015). Phylogenetic diversity of Amazonian tree communities. *Diversity and Distributions*, *21*, 1295–1307.

Ibarra-Manríquez, G., Cornejo-Tenorio, G., González-Castañeda, N., Piedra-Malagón, E. M., & Luna, A. (2012). El género *Ficus* L. (Moraceae) en México [The *Ficus* L. genus (Moraceae) in Mexico]. *Botanical Sciences*, *90*, 389–452.

Kadmon, R., & Allouche, O. (2007). Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: A unification of island biogeography and niche theory. *The American Naturalist*, *170*, 443–454.

Kembel, S.W., Cowan, P. D., Helmus, M., Cornwell, W. K., Morlon, H., Ackerly, D. D., . . . Webb, C. O. (2010). Picante: R tools for integration phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.

Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo, J. P., . . . D'Angelo, S. (2006). Rapid decay of tree community composition in Amazonian forest fragments. *Proceedings of National Academy of Sciences of the United States of America*, *103*, 19010–19014.

Laurance, W. F., & Yensen, E. (1991). Predicting the impact of edge effects in fragmented habitats. *Biodiversity and Conservation*, *55*, 72–92.

Letcher, S. G. (2010). Phylogenetic structure of angiosperms during tropical forest succession. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 97–104.

Lopes, A. V., Girão, L. C., Santos, B. A., Peres, C. A., & Tabarelli, M. (2009). Long-term erosion of tree reproductive trait diversity in edge-dominated Atlantic forest fragments. *Biological Conservation*, *142*, 1154–1165.

LPWG (2013) Legume phylogeny and classification in the 21st century: Progress, prospects and lessons for other species-rich clades. *Taxon*, *62*, 217–248.

Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015). A meta-calibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist*, *207*, 437–453.

Mas, J. F., & Correa, J. (2000). Analysis of landscape fragmentation in the ''Los Petenes'' protected area, Campeche, Mexico. *Investigaciones Geográficas*, *43*, 42–59.

Mazerolle, M. J., & Villard, M.-A. (1999). Patch characteristics and landscape context as predictors of species presence and abundance. *Ecoscience*, *6*, 117–124.

Mo, X.-X., Shi, L.-L., Zhang, Y. J., Zhu, H., & Slik, F. (2013). Changes in phylogenetic community structure during succession of traditional managed tropical rainforest in Southwest China. *PLoS One*, *8*, e71464.

Montiel, S., Estrada, A., & León, P. (2006). Bat assemblages in a naturally fragmented ecosystem in the Yucatan Peninsula, Mexico: Species richness, diversity and spatio-temporal dynamics. *Journal of Tropical Ecology*, *22*, 267–276.

Muellner-Riehl, A. N., Weeks, A., Clayton, J. W., Buerki, S., Nauheimer, L., Chiang, Y. C., . . . Pell, S. K. (2016). Molecular phylogenetics and molecular clock dating of Sapindales based on plastid *rbcL*, *atpB* and trnL-trnF DNA sequences. *Taxon*, *65*, 1019–1036.

Munguía-Rosas, M. A., Jurado-Dzib, S. G., Mezeta-Cob, C., Montiel, S., Rojas, A., & Pech-Canché, J. M. (2014). Continuous forest has greater taxonomic, functional and phylogenetic plant diversity than an adjacent naturally fragmented forest. *Journal of Tropical Ecology*, *30*, 323–333.

Munguía-Rosas, M. A., & Montiel, S. (2014). Patch size and isolation predict plant species density in a naturally fragmented forest. *PLoS One*, *9*, e111742.

Murcia, C. (1995). Edge effects in fragmented forest: Implications for conservation. *Trends in Ecology and Evolution*, *10*, 58–62.

Pennington, T. D., & Sarukhán, J. (2005). *Árboles tropicales de México: Manual para la identificación de las principales especies* [The tropical trees of Mexico: An identification manual of the main species]. Ciudad de México: UNAM-Fondo de Cultura Económica.

R Development Core Team (2015) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rezende, E., Lavabre, J. E., Guimarães, P., Jordano, P., & Bascompte, J. (2007). Non-random coextinctions in phylogenetically structured mutualistic network. *Nature*, *448*, 925–928.

Ribeiro, E. M. S., Santos, B., Arroyo-Rodríguez, V., Tabarelli, M., Souza, G., & Leal, I. R. (2016). Phylogenetic impoverishment of plant communities following chronic human disturbances in the Brazilian Caatinga. *Ecology*, 97, 1583–1592.

Rico-Gray, V. (1982). Estudio de la vegetación de la zona costera inundable del noreste del estado de Campeche, México: Los Petenes [Vegetation survey in the flooding coastal zone in northern Campeche, Mexico: The petenes]. *Biótica*, 7, 171–188.

Rico-Gray, V., & Palacios-Ríos, M. (1996). Salinidad y el nivel del agua como factores en la distribución de la vegetación en la ciénaga del NW de Campeche [Salinity and flooding as determinants of marsh vegetation distribution in NW Campeche]. *Acta Botánica Mexicana*, 34, 53–61.

Rosati, L., Fipaldini, M., Marignani, M., & Blasi, C. (2010). Effect of forest fragmentation on vascular plant diversity in a Mediterranean forest archipelago. *Plant Biosystems*, 144, 38–46.

Santos, B., Arroyo-Rodríguez, V., Moreno, C. E., & Tabarelli, M. (2010). Edge-related loss of tree phylogenetic diversity in the severely fragmented Brazilian Atlantic forest. *PLoS One*, 5, e12625.

Santos, B. A., Tabarelli, M., Melo, F. P. L., Camargo, J. L. C., Andrade, A., Laurance, S. G., & Laurance, W. (2014). Phylogenetic impoverishment of Amazonian tree communities in an experimental fragmented forest landscape. *PLoS One*, 9, e113109.

Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, 404, 72–73.

Swenson, N. (2009). Phylogenetic resolution and quantifying the phylogenetic diversity and dispersion of communities. *PLoS One*, 4, e4390.

Swenson, N. (2014). *Functional and phylogenetic ecology in R*. New York, NY: Springer.

Tabarelli, M., Lopes, A. V., & Peres, C. A. (2008). Edge-effects drive tropical forest fragments towards an early successional system. *Biotropica*, 40, 657–661.

Tamoya, H., Kajisa, T., Tagane, S., Mase, K., Chhang, P., Samreth, V., . . . Yahara, T. (2015). Effects of logging and recruitment on community phylogenetic structure in 32 permanent forest plots of Kampong Thom, Cambodia. *Philosophical Transactions of the Royal Society B*, 370, 20140008.

Tanentzap, A. J., & Lee, W. G. (2017). Evolutionary conservatism explains increasing relatedness of plant communities along a flooding gradient. *New Phytologist*, 213, 634–644.

Valdés, A., Lenoir, J., Gallet-Moron, E., Andrieu, E., Brunet, J., Chabrerie, O., . . . Decocq, G. (2015). The contribution of patch scale conditions is greater than that of macroclimate in explaining local plant diversity in fragmented forest across Europe. *Global Ecology and Biogeography*, 24, 1095–1105.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peternken, G., & Hermy, M. (2006). Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, 87, 542–548.

Webb, C. O. (2000). Exploring the phylogenetic structure of ecological communities: An example for rain forest trees. *The American Naturalist*, 156, 145–155.

Webb, C. O., Ackerly, D. D., & Kembel, S. W. (2008). Phylocom: Software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, 24, 2098–2100.

Webb, C. O., Ackerly, D. D., McPeek, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33, 475–505.

Wikström, N., Savolainen, V., & Chase, M. W. (2001). Evolution of the angiosperms: Calibrating the family tree. *Proceedings of the Royal Society B: Biological Sciences*, 268, 2211–2220.

Xu, W., Ci, X., Song, C., He, T., Zhang, W., Li, Q., & Li, J. (2016). Soil phosphorous heterogeneity promotes tree species diversity and phylogenetic clustering in a tropical seasonal rainforest. *Ecology and Evolution*, 6, 8719–8726.