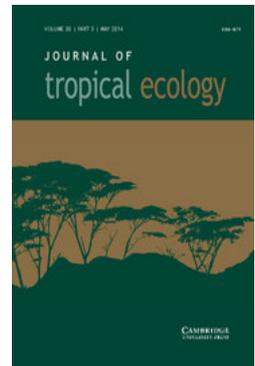


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Continuous forest has greater taxonomic, functional and phylogenetic plant diversity than an adjacent naturally fragmented forest

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Continuous forest has greater taxonomic, functional and phylogenetic plant diversity than an adjacent naturally fragmented forest

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Abstract: Several studies have evaluated the short-term effects of tropical forest fragmentation on plant taxonomic diversity, while only a few have evaluated its effects on functional or phylogenetic diversity. To our knowledge no study has looked at the long-term consequences of tropical forest fragmentation on the three main components of plant diversity simultaneously: taxonomic, functional and phylogenetic diversity. We sampled the vascular flora using belt transects (50 × 4 m) in a continuous tropical semi-evergreen forest (16 transects) and in an adjacent naturally fragmented forest (fragments of 1.7-My-old semi-evergreen forest immersed in a mangrove/sedge matrix) (18 transects), and compared their taxonomic, functional and phylogenetic plant diversity. There were 36 species in the continuous forest and 28 in the fragmented forest. Continuous forest was taxonomically more diverse (25%) than the fragmented forest. All functional diversity metrics were greater (6–33%) in the continuous than in the fragmented forest. Phylogenetic diversity was 19% greater and phylogenetically more overdispersed in the continuous forest than in the fragmented forest. The results suggest that in the fragmented forest not only is taxonomic plant diversity lower, but functional and phylogenetic diversity are as well. The negative effects of forest fragmentation on plant diversity seem to be chronic.

Key Words: diversity, forest fragmentation, functional diversity, Mexico, phylogenetic diversity, taxonomic diversity, tropical forest

INTRODUCTION

Forest fragmentation can be a natural or anthropogenic process resulting in the formation of isolated forest patches immersed in a matrix with a different plant composition (Laurance 1990, Laurance & Bierregaard 1997, Lovejoy *et al.* 1986). One of the most important threats to global diversity, anthropogenic forest fragmentation, exposes the organisms that remain in the fragment to the often hostile conditions of the ecosystem matrix (Laurance & Peres 2006, Murcia 1995). At the present rate of forest fragmentation, it is not difficult to predict that in a few decades most of the world's tropical forests will consist of small, isolated fragments; thus, it is crucial to determine the extent to which an isolated fragment can sustain representative diversity (Laurance 1991).

Most studies have assessed the effect of habitat fragmentation on diversity measured as taxonomic diversity (Fahrig 2003). However, taxonomic diversity is far from synonymous with biodiversity because it conveys little to no information about the functional role or the evolutionary history of species in a community (Swenson 2011). A more accurate assessment of diversity can be achieved by studying simultaneously the three main components of diversity: taxonomic, functional and phylogenetic diversity (Swenson 2011). Functional diversity can be defined as a variety of life-history traits presented by an assemblage of organisms (Mayfield *et al.* 2005), and is critical to the maintenance of ecosystem processes (Hooper & Vitousek 1997, Tilman & Downing 1994, Tilman *et al.* 1997). Phylogenetic diversity describes the total phylogenetic distance among species in a community (Faith 1992) and provides a measure of future biodiversity (Faith *et al.* 2010). Although a few studies have looked at the effects of tropical forest fragmentation on functional (Girão *et al.*

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2007, Santos *et al.* 2007) and phylogenetic plant diversity (Arroyo-Rodríguez *et al.* 2012, Santos *et al.* 2010) separately, we do not know of any study assessing the effects of fragmentation on these three main components of plant diversity simultaneously.

Previous studies looking at the impact of forest fragmentation on functional (Girão *et al.* 2007, Santos *et al.* 2007) and phylogenetic diversity (Arroyo-Rodríguez *et al.* 2012, Santos *et al.* 2010) of tropical plants have focused only on the recent effects of forest fragmentation (40- to 200-y-old fragments). However, many of the consequences require a sufficient relaxation period, with communities passing through a series of transitional states before final equilibrium conditions are reached (Helm *et al.* 2006, Terborgh *et al.* 1997, Tilman *et al.* 1994). In this sense, naturally fragmented ecosystems offer an enormous advantage over human-created fragmented forest because they have been fragmented for thousands or millions of years (Montiel *et al.* 2006, Watson & Peterson 1999).

In this study we compared taxonomic, functional and phylogenetic diversity between a continuous and an adjacent naturally fragmented forest (1.7 My old; CONANP-SEMARNAT 2006). Our objective was to compare the three main components of plant diversity between the continuous and fragmented forests to infer the potential effects of long-term forest fragmentation on plant diversity. We predict lower taxonomic, functional and phylogenetic diversity in the fragmented forest relative to that of the continuous forest because previous studies have shown that many plant species disappear from fragmented forest, especially emergent trees and shade-tolerant species (Laurance *et al.* 2000, Tabarelli *et al.* 2012). Furthermore, species inhabiting fragments are more heavily influenced by the environmental filters imposed by the matrix (high radiation, heat, desiccation, etc.). As a result, plant assemblages in the fragments may become dominated by pioneer-like species sharing functional traits such as fast growth and high light demand (Laurance *et al.* 2006), which would result in low functional diversity. Finally, as the traits that make plants more prone to extinction can be phylogenetically non-random (Vamossi & Wilson 2008), entire clades could be lost, thus reducing phylogenetic diversity.

METHODS

Study area

The study area is a belt of narrow vegetation (90°20'–90°29' W) located along the western coast of the Yucatan Peninsula (Rico-Gray 1982). The weather is warm sub-humid with seasonal rains (June–September), precipitation is 1000–1200 mm y⁻¹ and mean

temperature is 26.1–27.8 °C (Durán 1987a, Zamora 1999). The northern and central part of this region (20–21°N, c. 130 000 ha) has circular and semi-circular fragments of distinctive vegetation (i.e. taller and more diverse) scattered throughout a matrix of wetlands with variable salinity levels (Barrera 1982). Locally, these fragments are called petenes and may represent a system endemic to this region (Rico-Gray 1982). The vegetation is on Quaternary geological formations of approximately 1.7 My (CONANP-SEMARNAT 2006). It is believed that the higher elevation of these forested fragments relative to the matrix explains their presence, along with the fact that they usually have a permanent freshwater supply from a sinkhole (cenote) located in the centre of each fragment (Barrera 1982, Rico-Gray 1982). In the southern part of this region (19–20°N; c. 1000 ha) the forest becomes continuous. This area is a nature reserve under government protection and no activity that is incompatible with conservation is allowed.

Vegetation of the fragments and in the continuous forest is mainly dry and semi-evergreen tropical forest, with *Manilkara zapota*, *Metopium brownei*, *Bursera simaruba* as the dominant trees, while *Bravaisia tubiflora* and *Sabal yapa* dominate the understory (Durán 1987a, b, Rico-Gray 1982, Zamora 1999). Some fragments may also be dominated by tall mangrove trees such as *Laguncularia racemosa* and *Avicennia germinans* (Durán 1987a, b). In the fragmented forest the matrix is dominated by shorter mangroves (*Rhizophora mangle*, *Conocarpus erectus*) sedges (*Eleocharis cellulosa* and *Cladium jamaicense*) and cattails (*Typha dominguensis*) (Durán 1987a, b; Rico-Gray 1982).

Field work and sampling design

We selected a representative section (20°07'–20°14' N; 90°20'–90°29' W) of the fragmented forest where a gravel road provided access to seven forest fragments (Figure 1a). A representative section (19°54'–20°00' N; 90°20'–90°29' W) of the continuous forest was also delimited (Figure 1b). These were sampled from January to August 2013 using belt transects (50 × 4 m = 200 m²). In the fragmented forest a group of three transects (20 m apart) was set up per fragment in six different fragments (18 transects in total, equivalent to 3600 m²) (Figure 1a). Transects in this forest were not set up in randomly selected fragments because only a small number of fragments (n = 7) were accessible. No more than three transects were placed in each fragment owing to their small size. Five or six transects were systematically placed in the continuous forest (20 m apart and in a previously defined direction) at three different random points (16 transects in total, equivalent to 3200 m²) (Figure 1b). More sampling points were placed in the

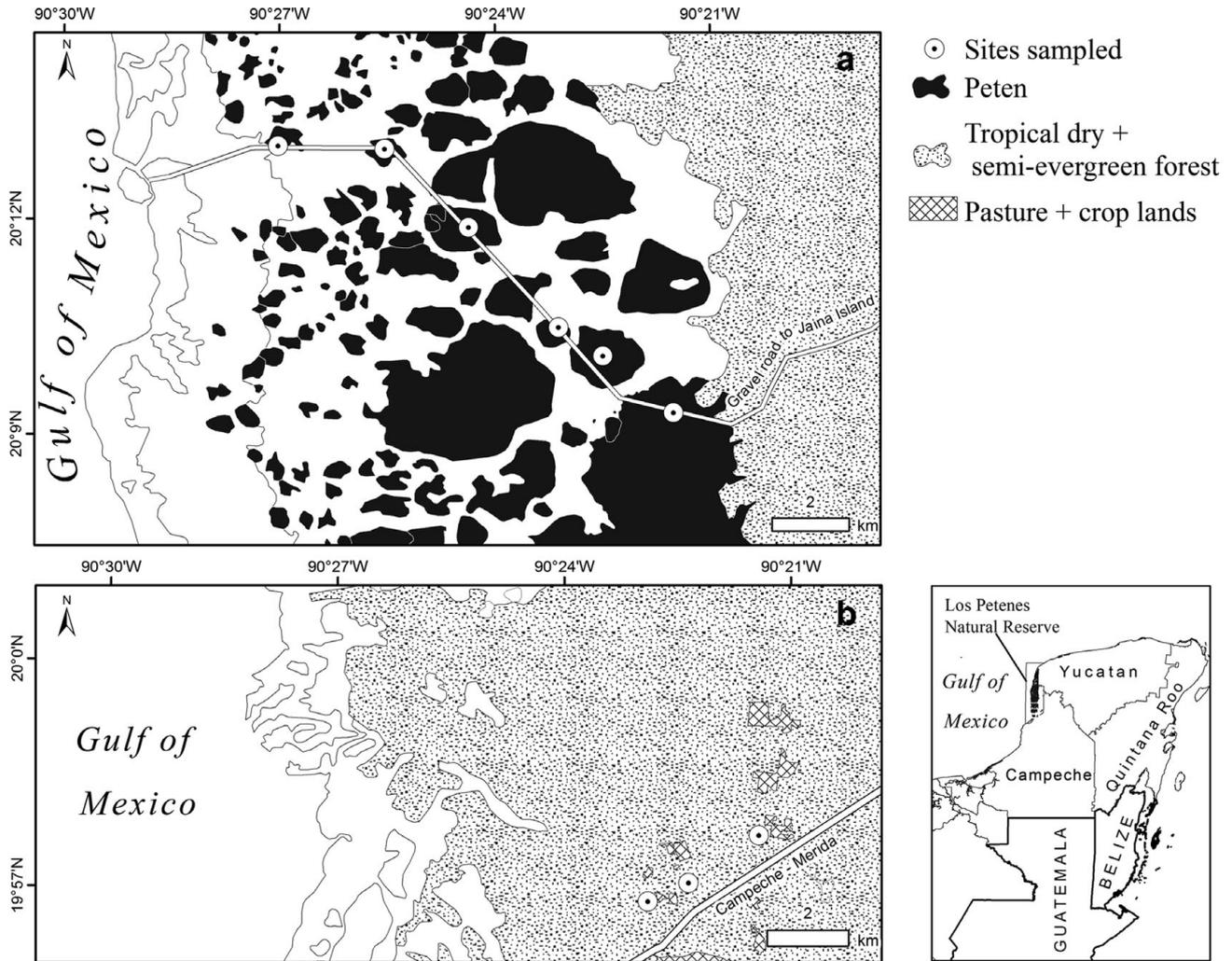


Figure 1. Map of the fragmented forest (a) and the continuous forest (b). Continuous forest is shown in the dotted pattern and vegetation fragments (petenes) are in black. There were more transects per sampling site in the continuous forest (5–6) than in the vegetation fragments (3) owing to the limited size of the latter. Details of the position of the two polygons and the nature reserve on the Yucatan Peninsula are also shown.

fragmented forest than in the continuous forest owing to the small size of the fragments.

To assess plant species richness and abundance, all plants with a girth larger than 5 cm (dbh = 1.6 cm) were recorded. Epiphytes, lianas, aquatic and secondary vegetation were not included in the vegetation survey because of the difficulties recording their abundance and obtaining information about their functional traits. For all plants recorded, dbh and life form were taken in situ. Unidentified species ($n = 4$ species) were morphotyped.

Species richness and taxonomic diversity

To assess the representativeness of observed species richness relative to expected richness we built species

accumulation curves for the two landscapes using the random method with 1000 permutations (Gotelli & Colwell 2011). Additionally, we calculated one incidence-based (Chao2) and two abundance-based (Chao1, ACE) species richness non-parametric estimators following the suggestion of Hortal *et al.* (2006) who recommended the use of several estimators together. As the forests differ moderately in the number of individuals sampled, we compared species richness using individual-based rarefaction curves (Gotelli & Colwell 2011). Species similarity between the two forests was assessed with Sørensen's similarity index. Taxonomic species diversity was assessed with the effective number of species or true diversity (Jost 2006), and species evenness with Pielou's index. All analyses were run in R3.0 software using the Vegan package (Dixon 2003).

Functional traits and functional diversity

Leaf functional traits (dry mass, punch strength, size, specific area and thickness) were recorded for at least two healthy, unshaded adults from 28 different species (Cornelissen *et al.* 2003). Additionally, maximum plant height for these 28 species were obtained from local floras (Brokaw *et al.* 2011, Pennington & Sarukhán 2005) and herbarium specimens, or measurements were taken in the field (shorter species only). For leaf traits five intact, fully exposed leaves (except understorey species) were collected per plant species. Species for which fewer than two individuals were accessible to collect samples were not included in the analysis. We obtained all functional traits for 25 and 22 species in the continuous and in the fragmented forest respectively. The abundance of all these species together represents 94% and 98% of all plants recorded in the continuous and the fragmented forest respectively. Leaf dry matter content was estimated as the dry weight of a previously dried leaf. Punch strength was measured as the weight needed for a 1-mm-diameter metal cylinder to penetrate a leaf. Leaf thickness was measured on fresh leaves with a digital caliper. Specific leaf area was measured as the one-side area of a fresh leaf with a foliar area meter (LI-COR LI-3000A) divided by its dry mass. The functional traits chosen are related to the environmental filters we believe are relevant in the study system. Leaf dry mass and plant height are negatively associated with environmental disturbances (Cornelissen *et al.* 2003), leaf size is negatively associated with environmental stress (e.g. heat, drought, high radiation; Cornelissen *et al.* 2003), leaf punch strength is positively associated with resistance to biotic damage (e.g. herbivores; Coley 1983, Feeny 1970), leaf thickness is positively correlated with thermal buffering and photosynthetic compound content (Niinemets 2001), and specific leaf area is positively correlated with nutrient/light availability in wetlands (Balun 2011).

Using the species-by-trait matrix we calculated some multidimensional functional diversity indices. The first metric calculated was Rao's quadratic entropy, which is the sum of the distances between pairs of species in a functional space weighted by the product of their abundance. This index was standardized by dividing the distance by the maximum possible distance so this index is bounded to a maximum of 1 (Botta-Dukát 2005). Also, we calculated a group of three metrics: functional richness, evenness and divergence, which describe independent and complementary components of functional diversity (Mouchet *et al.* 2010, Villéger *et al.* 2008). Functional richness was measured as convex hull volume and represents the functional space occupied by a species assemblage. In contrast to functional evenness and functional divergence, functional richness

cannot account for species abundance (Villéger *et al.* 2008). Functional richness was standardized by the global functional richness that includes all species, so that functional richness is constrained between 0 and 1. Functional evenness combines both the evenness of species spacing in a functional trait space and the evenness of species abundance; this index is 1 if all species have equal abundance and tends to zero as unevenness increases (Villéger *et al.* 2008). Functional divergence is the degree to which the most abundant taxa are away from the centroid of the functional trait space and is high when the most abundant species have extreme values (Villéger *et al.* 2008). Finally, we calculated per-trait community-level abundance-weighted and unweighted means using untransformed trait values to assess which traits are different between forests and whether any differences detected are attributable to abundance (change in weighted mean) or species turnover (change in unweighted means). This metric expresses the dominant trait value in the community (Lavorel *et al.* 2008).

Phylogenetic diversity

We first obtained a complete species list with the families following APG III (2009). Morphotyped species were excluded from the list because their phylogenetic position could not be accurately resolved. A fern, a bromeliad and one sedge species were also excluded because these would contribute disproportionately to phylogenetic diversity metrics owing to the low relatedness to the majority of species, as recommended by Arroyo-Rodríguez *et al.* (2012). Finally, the species list comprised 31 species in the continuous forest and 24 species in the fragmented forest, with only four and five species excluded for the fragmented and the continuous forest respectively. We created a time-calibrated phylogeny (in millions of years) using the PHYLOMATIC function of Phylocom 4.1 (Webb *et al.* 2008) based on the dated tree from Davis *et al.* (2004) for seed plants. The phylogeny obtained was rooted, completely dichotomous and ultrametric.

We uploaded the phylogeny into R 3.0 software and calculated the abundance-weighted version of the following metrics using the Picante package (Kembel *et al.* 2010): phylogenetic diversity, mean phylogenetic distance (MPD), mean nearest taxon phylogenetic distance (MNTD), net relatedness index (NRI) and nearest taxon index (NTI). Phylogenetic diversity is the sum of all branch lengths on the phylogenetic tree (Faith 1992). MPD is the average pairwise distance between each of the species in the phylogeny (Vamosi *et al.* 2009). MNTD is the mean distance between each species in the phylogeny and its most closely related species in the community (Vamosi *et al.* 2009). MPD and MNTD are complementary metrics to phylogenetic diversity. While the latter gives

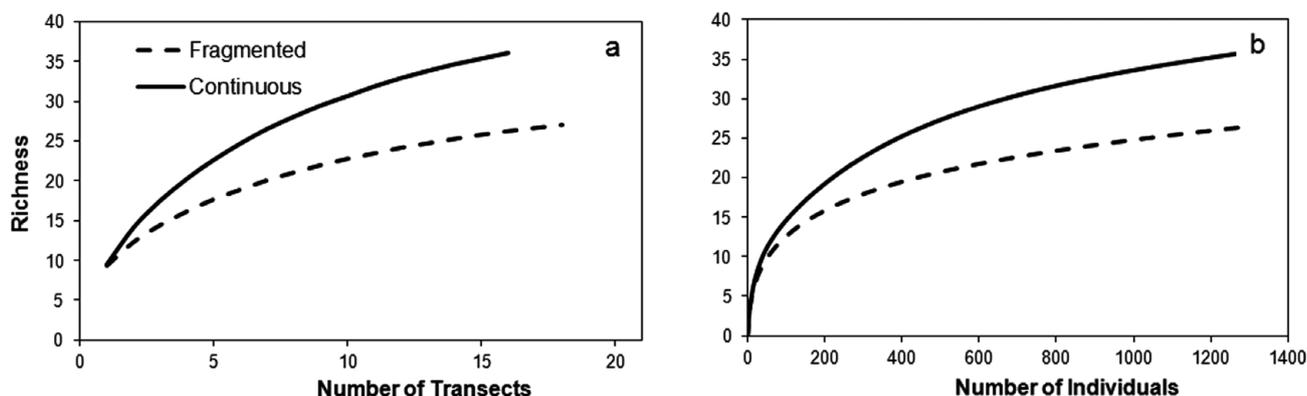


Figure 2. Species accumulation curve (a) and rarefaction curve (b) for plants in a continuous and a fragmented forest of the Yucatan Peninsula. Species accumulation curves were based on data from transects, while rarefaction curves were generated based on the number of individuals.

us an idea of the total branch length in the phylogeny of the community, together MPD and MNTD give an idea of how phylogenetically clustered the species in the community are (Webb *et al.* 2002). NRI and NTI are standardized MPD and MNTD respectively and thus, are easier to interpret than original values. Positive values of NRI and NTI indicate terminal and familial phylogenetic clustering respectively while negative values represent phylogenetic overdispersion (Webb *et al.* 2002). All of these metrics are measured in millions of years except NRI and NTI, which are in units of standard deviation. For all the metrics mentioned above (except NRI and NTI) standard error was calculated after 999 randomizations.

RESULTS

Taxonomic diversity

The species accumulation curve reached its asymptote in the fragmented forest, and nearly reached the asymptote in the continuous forest (Figure 2a). A total of 36 and 28 species were recorded in the continuous and the fragmented forest respectively (Appendix 1). The communities of the two forests had a similarity of 60% (Sørensen) in species composition. Richness estimated by non-parametric estimators averaged 43 ± 1 (hereafter mean ± 1 SE) species in the continuous forest; thus, the percentage represented by observed richness is 84% (Table 1). The fragmented forest's estimators suggested, on average, a species richness of 33 ± 1 ; therefore, observed species richness also represents 84% (Table 1). According to rarefaction curves, the forests started becoming evidently different, in terms of species richness, after 100 individuals with maximum differences occurring when 1305 individuals had been collected, the point at which we expected to find 36 ± 0.2 species in the continuous forest and only 26 ± 1.1 species in the

Table 1. Values of three asymptotic richness estimators (value \pm SE) and the percentage represented by the observed species richness (%) for a continuous and a fragmented forest on the Yucatan Peninsula, Mexico. Averages are given at the foot of the table.

Estimator	Continuous		Fragmented	
	Value \pm SE	%	Value \pm SE	%
Chao1	45 ± 12	80	33 ± 8	84
ACE	42 ± 3	86	35 ± 3	80
Chao2	44 ± 6	82	32 ± 5	87
Average	43 ± 1	84	33 ± 1	84

Table 2. Functional diversity measured as Rao's quadratic entropy (Rao's Q), functional richness, functional evenness and functional divergence of plants in a continuous and a fragmented forest on the Yucatan Peninsula, Mexico.

Metric	Continuous	Fragmented
Rao's Q	0.52	0.4
Functional richness	0.36	0.27
Functional evenness	0.35	0.33
Functional divergence	0.75	0.71

fragmented forest (Figure 2b). True diversity (1D) was 35% greater in the continuous forest (${}^1D = 8.17$) than in the fragmented forest (${}^1D = 6.05$). Pielou's evenness for the continuous forest (0.6) was 20% greater than that of the fragmented forest (0.5).

Functional diversity

Functional richness (33%), Rao's Q (11%), functional evenness (6%) and functional divergence (6%) were all greater in the continuous forest than in the fragmented forest (Table 2). For abundance-weighted means, the greatest differences between continuous and fragmented forest were found for leaf size (27% greater in continuous forest) and leaf punch strength (19% lower in continuous forest). Although a large difference between forests was

Table 3. Community-level abundance-weighted and unweighted means (± 1 SE) of plant functional trait values (Trait) in a continuous and a fragmented forest on the Yucatan Peninsula, Mexico. The percentages of change in values (continuous vs. fragmented; % Δ) are also shown for weighted and unweighted means.

Trait	Weighted			Unweighted		
	Continuous	Fragmented	% Δ	Continuous	Fragmented	% Δ
Leaf dry matter content (g)	0.34 \pm 0.02	0.34 \pm 0.02	0	0.4 \pm 0.1	0.4 \pm 0.1	0
Punch strength (g)	26 \pm 2	31 \pm 3	19	26 \pm 5	35 \pm 6	35
Leaf size (cm ²)	164 \pm 25	119 \pm 20	27	62 \pm 22	64 \pm 26	3
Leaf thickness (mm)	0.37 \pm 0.04	0.35 \pm 0.04	5	0.27 \pm 0.03	0.34 \pm 0.04	26
Plant height (m)	6.35 \pm 0.48	6.32 \pm 0.6	0.5	8 \pm 0.4	8 \pm 0.6	0
Specific leaf area (cm ² g ⁻¹)	469 \pm 123	341 \pm 111	27.3	177 \pm 61	179 \pm 73	1

Table 4. Phylogenetic diversity, mean phylogenetic distance (MPD), mean nearest taxon distance (MNTD), net relatedness index (NRI) and nearest taxon index (± 1 SE) in a continuous and a fragmented forest. Phylogenetic diversity, MPD and MNTD are in millions of years (My) and NRI and NTI are in standard deviations of MPD and MNTD, respectively.

Metric	Continuous	Fragmented
Phylogenetic diversity (My)	2320 \pm 13.5	1940 \pm 19.5
MPD (My)	191 \pm 3	166 \pm 3
MNTD (My)	175 \pm 6	114 \pm 7
NRI (SD)	-1.87	-0.44
NTI (SD)	-1.86	0.33

found for specific leaf area (27.3%), there was a big overlap in standard errors (Table 3). The rest of the traits (dry matter content, leaf thickness and plant height) showed only minor differences between forests (0–5%; Table 3). The greatest differences in unweighted means between the continuous and fragmented forests were recorded for leaf punch strength (35% lower in the continuous forest) and leaf thickness (26% lower in the continuous forest), while there was only minimal variation (1–3%) in the remaining traits (dry matter content, leaf size, plant height and specific leaf area) (Table 3).

Phylogenetic diversity

MNTD (54%), phylogenetic diversity (19%) and MPD (15%) were all greater in the continuous than in the fragmented forest (Table 4). NRI was negative and substantially lower (325%) for the continuous forest than for the fragmented forest (Table 4). Finally, NTI went from slightly positive (0.33) in the fragmented forest to negative (-1.86) in the continuous forest (Table 4).

DISCUSSION

The results of our study show that all three of the main components of plant diversity – taxonomic, functional

and phylogenetic diversity (Swenson 2011) – are consistently lower in the fragmented forest relative to the continuous forest. We will elaborate on the mechanisms which could explain the observed negative effects of forest fragmentation on each component of plant diversity.

Although the number of species reported in the continuous (36) and fragmented (28) forest are apparently low, the fact that the cumulative species curves nearly reached their asymptotes and that we recorded 84% of species predicted by the estimators makes us think that species richness is well represented (with the exception of epiphytes and lianas, which were not included in our sampling). Previous studies had reported that plant species richness in the study area was low compared with that of other tropical forests in Mexico (Durán 1987a); however, this can be considered an additional advantage of using this area as a study model to look at the effects of forest fragmentation on plant diversity because less sampling effort is needed to obtain a good representation of plant diversity. It is not surprising that taxonomic diversity was lower in the fragmented forest because it is well known that tropical forest fragmentation negatively affects plant population size, reduces dispersal (pollen and propagules), and exposes individuals on the edge to the inhospitable environmental conditions prevailing in the matrix (Laurance & Bierregaard 1997). Although previous work has suggested that plant species richness may respond slowly to forest fragmentation (Helm *et al.* 2006), most studies have looked at plant taxonomic diversity in recently formed fragments (Arroyo-Rodríguez *et al.* 2008). Therefore, a major contribution of our paper is that we assessed taxonomic plant diversity in a forest which has been fragmented for very long time (1.7 My).

Similar to taxonomic diversity, all functional diversity metrics were lower in the fragmented than in the continuous forest. Functional richness, evenness and divergence are complementary metrics which give us an idea about the size and configuration of the functional space of a community (Villéger *et al.* 2008). Our results suggest that the functional space occupied is larger (i.e. greater functional richness), more evenly distributed (i.e.

greater functional evenness), and the distance from the most abundant taxa to the centroid of the functional space is greater (i.e. greater functional divergence) in the plant community of the continuous forest than it is in the community of the fragmented forest. Rao's quadratic entropy is an independent measure of functional diversity that suggests that functional diversity is greater (11%) in the continuous forest. We suggest that the reason the community in the fragmented landscape has lower functional diversity is that the environmental filters imposed by the matrix have selected those species able to cope with these filters, especially on the edges of the forest fragments. The matrix in our study system is represented by a wetland with a level of salinity in which only a mix of mangroves, cattails and sedges can survive (Rico-Gray 1982). The habitat of mangroves is recognized as a highly stressful environment where environmental filters such as high radiation, heat, salinity, and low oxygen and nutrient (N, P) availability (Balun 2011) filter species tolerant to these environmental conditions. Also, the vegetation of the matrix is shorter than that of the fragments; the latter is thus beaten by winds and storms, especially the species growing at the edge. Owing to the larger edge-area ratio in the fragmented forest, it is expected that its plant community would be more exposed to the environmental filters prevailing in the matrix (higher radiation, heat, salinity as well as lower oxygen and nutrient availability) than the community of the continuous forest would be and therefore, it is functionally narrower than the continuous forest. Reduced plant functional diversity in fragmented forests has been also reported for other tropical forests in South America (Girão *et al.* 2007, Santos *et al.* 2007) and some authors have documented the negative effects of tropical forest fragmentation on functional diversity in other taxonomic groups (e.g. insects; Barragán *et al.* 2011).

Abundance-weighted and unweighted means of functional traits are indicative of the main environmental filters and the traits that are being selected. In this study, punch strength (abundance-weighted and unweighted mean), leaf size (abundance-weighted mean) and leaf thickness (unweighted mean) showed the most striking differences between forests. Punch strength was higher in the fragmented than in the continuous forest, which also suggests that plant species are more resistant to physical (biotic and abiotic) damage in the fragmented forest, and that nutrient availability may be lower in this forest. Leaf size is negatively correlated with environmental stress (heat, drought and high radiation), therefore, the lower values of these traits in the fragmented forest suggest that the relatively reduced functional diversity of this system is at least partially due to the greater degree of environmental stress prevailing in this forest. On the other hand, leaf thickness was higher in the fragmented than in the continuous forest, which also suggests that

plant species in the fragmented forest tend to have greater thermal buffering and retain more photosynthates than plants in the continuous forest. The fact that some functional traits differed between the two forest types in abundance-weighted means and others in unweighted means suggests that the changes in some functional traits can be attributed to changes in abundance (leaf size) or in species composition (leaf thickness). For leaf punch strength both changes in abundance and species composition seem to be responsible for the differences between forests (i.e. abundance-weighted and unweighted means differ between forests).

Plant phylogenetic diversity was, in general, lower in the fragmented than in the continuous forest. Thus, we suggest that the fragmented forest has lost a relatively high amount of its phylogenetic history (i.e. phylogenetic diversity, MNTD and MPD in the fragmented forest were 380, 61 and 25 million years less than in the continuous forest). Also, the fact that NRI and NTI are more positive in the fragmented forest suggests that the plant community in the fragmented forest tends to be phylogenetically more clustered while the community of the continuous forest is phylogenetically more overdispersed (Webb *et al.* 2002). Some authors have suggested that high phylogenetic conservatism in plant traits associated with fragmentation vulnerability/resistance can produce the loss of entire clades as well as a reduction in the phylogenetic distance among the remaining species in the phylogeny (Arroyo-Rodríguez *et al.* 2012, Santos *et al.* 2010). This could be the case in the system we studied because, as shown in Figure 3, *Jacquinia* species are present in the continuous but absent from the fragmented forest; concomitantly, some of the older lineages present in the continuous forest are absent from the fragmented forest, and this may have also reduced phylogenetic diversity. Our results do not concur with previous studies in which the authors have shown that high values of phylogenetic diversity were maintained in a severely fragmented tropical forest of Mexico (Arroyo-Rodríguez *et al.* 2012) and in a tropical forest of Brazil (Santos *et al.* 2010). It is likely that these studies found no association between fragmentation and phylogenetic diversity because the region only became fragmented relatively recently (40–200 y ago). In contrast, our study region has been fragmented for 1.7 million years indicating that over this period phylogenetic diversity has been reduced substantially in the fragmented forest relative to the continuous forest.

Here we have shown that a forest that has been fragmented for a very long time has undergone a general erosion of plant diversity (taxonomic, functional and phylogenetic diversity) relative to an adjacent continuous forest. Some authors have pointed out that plant taxonomic diversity may respond slowly to forest fragmentation (Helm *et al.* 2006) and therefore, studies

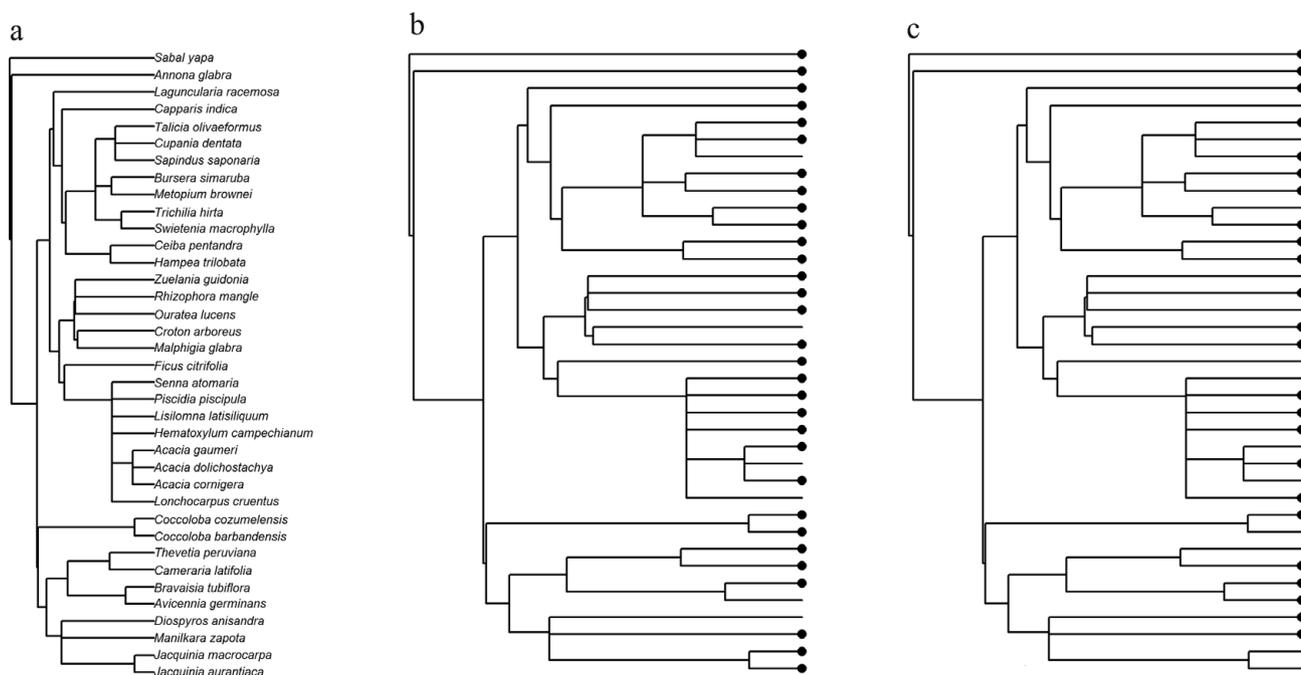


Figure 3. Phylogenies representing all of the species included in the analysis from a continuous and a fragmented forest on the Yucatan Peninsula (a), the species present in a continuous (b), and those in a fragmented forest (c). Species presence is indicated by a circle at the tip of the phylogeny.

looking at the short-term effects of forest fragmentation may underestimate the impact of forest fragmentation and depict a falsely optimistic future for plant diversity in forest fragments. In this sense, a naturally fragmented forest such as the one we studied may help us make relevant predictions regarding the fate of plant diversity in fragmented forests. According to our results it seems that, in the long term, species loss is not reversible if the forest patches remain disconnected. Short-term studies are still valuable for assessing the early responses of biodiversity to forest fragmentation; however, we recommend that future studies take into account the age of the fragments to detect whether the impact of fragmentation on plant biodiversity reported is time-dependent. Another important contribution of this study is the assessment of plant diversity in poorly understood components of diversity: functional and phylogenetic diversity. We know of only three studies that look at functional (Santos *et al.* 2007) and phylogenetic diversity (Arroyo-Rodríguez *et al.* 2012, Santos *et al.* 2010) in fragmented forests, but none assess the long-term effects of fragmentation. To date, research has identified that functional and phylogenetic diversity may not have the same response to forest fragmentation. For example, Santos and colleagues found a strong fragmentation effect on plant functional diversity (Santos *et al.* 2007), but no important effect on phylogenetic diversity (Santos *et al.* 2010) in Usina Sierra Grande, Brazil. We suspect that phylogenetic diversity only responds to long-term forest fragmentation, while functional diversity is sensitive

to both short- and long-term fragmentation. However, studies that simultaneously evaluate functional and phylogenetic diversity in forests with contrasting levels of fragmentation are scarce, thus no general conclusion can be reached in this regard yet.

In conclusion, taxonomic, functional and phylogenetic plant diversity is consistently lower in a fragmented forest relative to an adjacent continuous forest and this could be a chronic effect of long-term forest fragmentation. We encourage researchers to examine all three of the main components of diversity simultaneously in naturally fragmented forests in order to detect any patterns regarding the long-term effect of forest fragmentation on the different diversity components.

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Appendix 1. List of plant species found and their abundance in a continuous and a fragmented forest on the Yucatan Peninsula.

Species	Continuous	Fragmented
<i>Acacia cornigera</i> (L.) Willd.	5	0
<i>Acacia dolichostachya</i> S.F. Blake	0	8
<i>Acacia gaumeri</i> S.F. Blake	2	0
<i>Acrostichum aureum</i> L.	51	0
<i>Annona glabra</i> L.	5	1
<i>Avicennia germinans</i> (L.) Stearn	0	63
<i>Bonellia macrocarpa</i> ssp. <i>pungens</i> A. Gray	0	2
<i>Bravaisia tubiflora</i> Hemsl.	531	762
<i>Bromelia pinguin</i> L.	2	0
<i>Bursera simaruba</i> (L.) Sarg.	5	28
<i>Cameraria latifolia</i> L.	55	189
<i>Capparis indica</i> (L.) Druce	5	0
<i>Ceiba pentandra</i> (L.) Gaertn	88	5
<i>Cladium jamaicense</i> Crantz	0	29
<i>Coccoloba barbandensis</i> Hemsl.	3	0
<i>Coccoloba cozumelensis</i> Hemsl.	1	1
<i>Croton arboreus</i> Millsp.	0	1
<i>Cupania dentata</i> Glaz.	1	0
<i>Diospyros anisandra</i> S.F. Blake	0	2
<i>Ficus citrifolia</i> Mill.	1	0
<i>Haematoxylum campechianum</i> L.	3	1
<i>Hampea trilobata</i> Standl.	12	36
<i>Jacquinia aurantiaca</i> Ait.	1	0
<i>Jacquinia macrocarpa</i> Cav.	5	0
<i>Laguncularia racemosa</i> C.F. Gaertn.	1	1
<i>Lonchocarpus cruentus</i> Lundell	0	4
<i>Lysiloma latisiquum</i> (L.) Benth.	8	6
<i>Malpighia glabra</i> L.	3	11
<i>Manilkara zapota</i> (L.) Royen	79	70
<i>Metopium brownei</i> Urb.	77	156
<i>Ouratea lucens</i> Engl.	3	0
<i>Piscidia piscipula</i> (L.) Sarg.	48	12
<i>Rhizophora mangle</i> L.	4	2
<i>Sabal yapa</i> C. Wright ex Becc.	270	211
<i>Sapindus saponaria</i> Lam.	0	3
<i>Senna atomaria</i> (L.) H.S. Irwin & Barneby	19	0
<i>Swietenia macrophylla</i> King	2	9
<i>Talisia olivaeformis</i> (H.B.K.) Radlk	7	9
<i>Thevetia peruviana</i> K. Schum.	5	0
<i>Trichilia hirta</i> L.	3	0
<i>Zuelania guidonia</i> (SW.) Britton & Millsp.	1	0
Morphotype 1	1	1
Morphotype 2	0	1
Morphotype 3	1	0
Morphotype 4	1	0