

Maintenance of tree phylogenetic diversity in a highly fragmented rain forest

Víctor Arroyo-Rodríguez^{1*}, Jeannine Cavender-Bares², Federico Escobar³,
Felipe P. L. Melo⁴, Marcelo Tabarelli⁴ and Bráulio A. Santos^{1,4}

¹Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (UNAM), Morelia, Michoacán, Mexico; ²Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA; ³Red de Ecoetología, Instituto de Ecología A.C., AP 63, 91000, Xalapa, Veracruz, Mexico; and ⁴Departamento de Botânica, Universidade Federal de Pernambuco, Recife, PE 50670-901, Brazil

Summary

1. Deforestation and forest fragmentation can drive species to local extinction, potentially changing the phylogenetic community structure and diversity of remaining assemblages. We tested this hypothesis analysing a large vegetation data set from a highly fragmented rain forest.

2. We assessed 9000 trees (both saplings and adults) from 268 species in 45 rain forest patches (ranging from < 1 to 700 ha) in three landscapes with different deforestation levels (4%, 11%, and 24% forest cover) in Los Tuxtlas, Mexico. We tested whether species density (i.e. number of species per unit area) and phylogenetic structure and diversity differed among landscapes, whether they were related to patch area, and whether the relationships differed among landscapes.

3. Overall, the observed differences in sapling and adult species densities across forest patches and landscapes (e.g. lower species densities in smaller patches) resulted in few and very weak changes in the phylogenetic community structure and diversity. Our results indicate that local extirpation of tree species may occur randomly or uniformly (but not in a clustered manner) throughout the phylogenetic tree, supporting the hypothesis of low phylogenetic conservatism of traits associated with vulnerability to forest fragmentation in the Neotropics.

4. Synthesis. This study indicates that in highly deforested and fragmented rain forests, the local extirpation of tree species does not occur across entire lineages. These novel and hopeful findings have direct implications for the ecology and conservation of fragmented rain forests. The maintenance of phylogenetic diversity in highly fragmented landscapes suggests that ecosystem function and stability may be maintained despite the loss of a number of tree species. We argue that in this unique Neotropical region, both large and small rain forest patches are critical for conserving regional tree evolutionary history.

Key-words: evolutionary diversity, habitat fragmentation, Los Tuxtlas, Mexico, relatedness, taxonomy, trait conservatism

Introduction

Intensification of land use is considered the main driver of global biodiversity change in terrestrial ecosystems (Sala *et al.* 2000). Because a large proportion of global biodiversity is located in fragmented landscapes, biodiversity protection largely depends on maintaining biodiversity in these spatially heterogeneous landscapes (Fahrig *et al.* 2010). Both theoretical (reviewed by Haila 2002) and empirical (e.g. Santos *et al.* 2008; Arroyo-Rodríguez *et al.* 2009a; Pardini *et al.* 2010) studies evaluating species responses to changes in landscape spatial

pattern have increased; however, this topic is still controversial because of important methodological and theoretical caveats in fragmentation studies (Fahrig 2003; Lindenmayer *et al.* 2008). One important caveat in fragmentation studies is that most biodiversity assessments have been based on the number of species and/or their relative abundances, providing little information about the changes in phylogenetic relatedness of species and individuals within assemblages in fragmented ecosystems (but see Santos *et al.* 2010). This information is increasingly recognized as critical in biodiversity assessments (May 1990; Purvis & Hector 2000; Cavender-Bares *et al.* 2009; Cadotte *et al.* 2010), because it can be used to evaluate conservation priorities of particular taxa (e.g. Pavoine, Ollier & Dufour 2005), bridge gaps between ecological and

*Corresponding author. E-mail: victorarroyo_rodriguez@hotmail.com

evolutionary questions during forest succession (Letcher 2010), infer mechanisms of community assembly (reviewed by Webb *et al.* 2002; Cavender-Bares *et al.* 2009) and determine whether the evolutionary relationships among species of an assemblage affect ecological processes and ecosystem functioning (Webb *et al.* 2002; Cadotte, Cardinale & Oakley 2008).

Tropical forests have been the primary sources of new agricultural lands in recent decades (Gibbs *et al.* 2010) and are currently considered the most deforested and fragmented forests worldwide (FAO 2011). Tropical forests also represent the most species-rich biome on Earth and are highly diverse in terms of both species richness and phylogenetic composition. Although evidence indicates that a large proportion of regional native biodiversity may be maintained in deforested and fragmented tropical landscapes (Arroyo-Rodríguez *et al.* 2009a), changes in phylogenetic structure of tree assemblages in response to declining species richness in fragmented tropical landscapes are still poorly understood. Because species richness may depend on patch size (Rosenzweig 1995) and species–area relationships may vary among landscapes with different deforestation levels (Hill & Curran 2005; Arroyo-Rodríguez *et al.* 2009a; Pardini *et al.* 2010), it is necessary to adopt a landscape perspective to understand the compositional dynamics of fragmented forests. Furthermore, because the long lifespan of tropical trees (centuries) may prevent some fragmentation effects from being observed in recent (< 50 year) deforestation frontiers (Ewers & Didham 2006), both adult and sapling tree assemblages need to be assessed to better understanding community organization in fragmented forests.

Most tropical tree species are dispersed by animals (e.g. Gentry 1982). Large-bodied frugivorous mammals (> 1 kg) can disperse a high quantity of large-seeded species (> 1 cm in length) that have a limited assemblage of dispersal agents (e.g. Peres & van Roosmalen 2002; Stevenson, Pineda & Samper 2005). Because these mammals are at greater risk of local extinction in forest fragments (i.e. greater hunting pressures, lower reproductive rates, smaller population sizes, and in many

cases, larger home-range requirements; see Stoner *et al.* 2007), seed dispersal and seedling recruitment of large-seeded zoochorous tree species may be limited in fragmented forests (Melo, Dirzo & Tabarelli 2006; Melo *et al.* 2010). Furthermore, in small forest patches (< 10 ha) and along forest edges, notable changes in the microenvironmental conditions (e.g. higher temperature and light incidence, lower humidity) can increase tree mortality rates and reduce seed germination and seedling establishment of many late-successional shade-tolerant species (e.g. Laurance *et al.* 2002; González-Di Pierro *et al.* 2011). In fact, evidence from different fragmented rain forests indicates that the tree species that disappear first from forest remnants share similar life history traits (e.g. large-seeded, emergent, shade-tolerant, hardwood, and/or vertebrate-pollinated species; Silva & Tabarelli 2000; Laurance *et al.* 2006; Santos *et al.* 2008; Lopes *et al.* 2009).

This phenotypic clustering in species susceptibility to forest fragmentation may reduce the phylogenetic diversity of remaining assemblages if the traits are conserved phylogenetically (Webb *et al.* 2002; Cavender-Bares *et al.* 2004). Under this scenario of phylogenetic trait conservatism, entire clades could be lost and remaining individuals would tend to co-occur with close relatives, reducing the phylogenetic distance between them (Fig. 1a). Conversely, if traits associated with high vulnerability to forest fragmentation are phylogenetically convergent (i.e. evolved independently from distant-related ancestors), no lineage will be completely lost and few changes in pairwise phylogenetic distance are expected (Fig. 1b). The level of change in phylogenetic clustering or evenness imposed by deforestation and forest fragmentation will also depend on the phylogenetic structure of the original assemblage. For instance, if the original assemblage is phylogenetically even, such as old-growth terra firme forests of Peru (Fine & Kembel 2011) and Costa Rica (Letcher 2010), the local extirpation of phenotypically similar but unrelated species may cause remaining species to be more distantly related, increasing phylogenetic evenness.

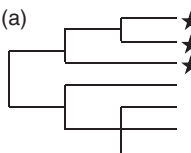
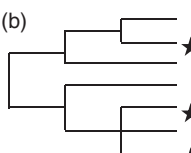
Original assemblage	Expected changes in phylogenetic diversity and structure	Expected changes in phylogenetic metrics
(a) 	<ol style="list-style-type: none"> 1) Loss of a large monophyletic clade 2) Reduced phylogenetic distance between species and individuals 3) Phylogenetic clustering increases 	<p>Lower MPD and MNTD. Higher NRI and NTI.</p>
(b) 	<ol style="list-style-type: none"> 1) Species loss is randomly distributed throughout the phylogeny 2) Phylogenetic distances between species are little affected or increase 3) Phylogenetic evenness shows little change or increases 	<p>No change or higher MPD and MNTD. No change or lower NRI and NTI.</p>

Fig. 1. Two (of multiple) possible scenarios of changes in community phylogenetic diversity and structure associated with species extinction. A total of three species are lost in both cases (indicated with stars). The expected changes in the phylogenetic metrics analysed in the present study are also indicated (see Methods for a detailed description of these metrics).

We tested these alternative hypotheses using a large vegetation data set from 45 rain forest patches located in three landscapes with different deforestation levels (4%, 11%, and 24% forest cover) in the Los Tuxtlas region of Mexico. Particularly, we tested whether species density (i.e. number of species per unit area), and phylogenetic structure and diversity differed among landscapes, whether they were related to patch area, and whether the relationships differed among landscapes. Because the Los Tuxtlas region was fragmented recently (ca. 40–50 year ago), the extinction of many species may not be evident in adult assemblages. We, therefore, carried out the analyses considering (i) the sapling assemblage (plant individuals ranging from 2.5 to 10 cm dbh) and (ii) the adult assemblage (trees with dbh > 10 cm). Our study demonstrates that in strongly deforested and fragmented rain forests, changes in tree species density among forest patches and landscapes result in few and very weak changes in the phylogenetic diversity and structure of remaining tree assemblages. This novel and hopeful finding supports the hypothesis of low phylogenetic conservatism of traits associated with vulnerability to forest fragmentation in the Neotropics and has direct implications for the ecology and conservation of fragmented rain forests.

Materials and methods

STUDY SITES

The Los Tuxtlas region is in south-eastern Veracruz State, Mexico (18° 27'–18°45'N; 94°37'–95°22'W). The climate is warm and humid, with a mean annual temperature of 25 °C and annual rainfall between 3000 and 4600 mm. The elevation ranges from 0 to 1780 m asl. Los Tuxtlas was decreed a Biosphere Reserve in 1998 because of its high biodiversity. The reserve is 155 122 ha and is immersed within the Mexican Transition Zone, characterized by the mixed biogeographical origin of its biota, which is comprised of elements of both northern and Neotropical origin (Rzedowski 1978). In fact, the region represents the northern limit of tropical rain forest distribution in the Neotropics (Dirzo & García 1992). The original dominant vegetation type (below 700 m asl) was tropical rain forest, but the area has been heavily deforested and fragmented since the 1970s, and the remaining rain forest is surrounded by a matrix of pastures and croplands (Castillo-Campos & Laborde 2004).

Elsewhere, we have presented detailed descriptions of the three fragmented landscapes we studied in Los Tuxtlas (e.g. Arroyo-Rodríguez *et al.* 2007, 2009a), hence only a brief overview is given here. The landscapes, situated between 0 and 400 m asl, represent a gradient of deforestation and are of a similar overall land area (about 5000 ha). They are naturally delimited by the coast and large rivers and separated approximately 30 km from each other. We digitized the landscapes in ArcView 3.2 on the basis of aerial photographs (1 : 20 000), orthophotos and field information. The landscape with the lowest deforestation level (LDL) was 5356 ha, 24% of which was rain forest distributed among 75 patches ranging from 0.5 to 700 ha (median size 3.2 ha); the landscape with intermediate deforestation level (IDL) was 4965 ha, 11% of which was rain forest distributed among 88 patches (median size 2.6 ha, range 0.5–76 ha); and the landscape with the highest deforestation level (HDL) covered 5046 ha, 4% of which

was rain forest distributed among 46 patches (median size 2.0 ha, range 0.5–68 ha). Detailed maps of the study landscapes are reported in Arroyo-Rodríguez *et al.* (2007, 2009a).

DATA COLLECTION

We used the Gentry's (1982) protocol to sample vegetation in 45 randomly selected forest patches (15 per landscape). We sampled 0.1 ha within each patch using 10 randomly located 50 × 2 m plots. We recorded all species of trees, shrubs, lianas, palms and herbs (i.e. Heliconiaceae) with a diameter at breast height (dbh) ≥ 2.5 cm (Arroyo-Rodríguez *et al.* 2009a). However, we excluded lianas and herbs in the phylogenetic analyses because 27% of the lianas species were not identified (i.e. they were classified as morphospecies in the previous analyses; Arroyo-Rodríguez & Toledo-Aceves 2009), and herbs are rare in the sites (see Arroyo-Rodríguez *et al.* 2009b) and would contribute disproportionately to phylogenetic structure owing to their low relatedness to the majority of species. In general, the tree inventory was reasonably accurate with our sampling effort, with 84–90% of the species recorded in each landscape (see Table S1 in Supporting Information).

ANALYTICAL METHODS

For each forest patch, we calculated four abundance-based phylogenetic metrics (Webb *et al.* 2002; Webb, Ackerly & Kembel 2008; Vamوسي *et al.* 2009): mean phylogenetic distance (MPD), mean nearest taxon phylogenetic distance (MNTD), net related index (NRI) and nearest taxon index (NTI). MPD measures the average phylogenetic distance among pairs of individuals drawn at random from a sample (including conspecifics); MNTD does the same, but the distance is measured to the closest non-conspecific relative (Webb, Ackerly & Kembel 2008; Vamوسي *et al.* 2009). NRI is a calculation of the effect size of MPD relative to a null model and indicates whether taxa in a sample are more phylogenetically clustered (positive NRI) or even (negative NRI) than expected at random; NTI quantifies the extent of terminal clustering, that is, intrafamilial clustering (positive NTI also indicates phylogenetic clustering, while negative values represent phylogenetic evenness).

We first produced a full species list based on the APG III (2009) classification after identifying the 9000 trees sampled in the 45 plots. We then classified species by genus and family – we recorded 268 species belonging to 166 genera and 55 families – and used the `PHYLOMATIC` function of Phylocom 4.1 (Webb, Ackerly & Kembel 2008) and a maximally resolved supertree of angiosperms (R20091110 available at <http://www.phylodiversity.net>) to assemble the species list into a phylogeny (i.e. the regional phylogeny). The regional phylogeny had branch lengths estimated with the `BLADJ` algorithm and the node ages provided by Wikström, Savolainen & Chase (2001). After constructing the time-calibrated phylogeny of our study area, we used the `COMSTRUCT` function of Phylocom 4.1 to calculate the phylogenetic metrics for each sample. Because the remaining tree assemblages tend to become increasingly dominated by a small group of species (e.g. Laurance *et al.* 2006, 2011), the switch '-a' was used to weight phylogenetic distances by taxa abundances.

To determine whether the phylogenetic structure of forest patches differed from the community phylogenetic structure expected by chance, we compared observed phylogenetic distances among individuals (MPD and MNTD) to the expected phylogenetic distances for 999 randomly generated null communities (MPD.rnd and MNTD.rnd, respectively). We used null model 2 of Phylocom 4.1 to

generate null communities. In this model, species in each sample become random draws from the phylogeny pool (Webb, Ackerly & Kembel 2008). The null model has the advantage of maintaining the species richness and abundance structure within communities. It assumes that all species of the pool are equally able to colonize any forest patch within the study area. After computing observed and expected MPD and MNTD for each sample, we calculated NRI and NTI metrics, which are standardized metrics of MPD and MNTD, respectively (Webb *et al.* 2002; Webb, Ackerly & Kembel 2008). We reported MPD and MNTD in millions of years and NRI and NTI in units of standard deviation.

We used the `nodesig` procedure of Phylocom 4.1 (Webb, Ackerly & Kembel 2008) to identify clades that contribute significantly to non-random phylogenetic structure of both adult and sapling assemblages in each forest patch. Based on a randomization test, `nodesig` assesses whether a particular node in the sample has significantly more or less descendent taxa than expected by a null model. This null model is based on random draws of n taxa from the terminals of the regional phylogeny, where n is the number of taxa in the sample. Nodes with more or fewer descendent taxa than expected by chance are referred to as 'sigmore' or 'sigless'. They allowed us to determine which clades are responsible for the non-random phylogenetic structure of the sampled assemblage (Webb, Ackerly & Kembel 2008).

To test whether tree species extirpation from forest patches changes the phylogenetic structure and phylogenetic diversity of remaining assemblages, we first tested for patch area effects on species density (species per 0.1 ha) among landscapes through a generalized linear model, with the landscape as a fixed factor and patch size as a fixed covariable (Species density = Landscape + Patch size + Landscape \times Patch size). This same method was used to test for differences in stem density among different-sized forest patches and landscapes, to assess whether differences in species density are related to differences in stem density (see Table S2 and Fig. S1). As suggested for count-

dependent variables (i.e. species density and stem density), we selected a Poisson distribution with a log-link function and corrected for overdispersion of the data (Crawley 2002). We conducted this analysis for sapling and adult tree assemblages separately. When we found differences among landscapes, we used contrast tests to identify which landscapes differed from each other (Crawley 2002). A similar statistical procedure was used to assess changes in phylogenetic metrics among landscapes and patches of different sizes (MPD, MNTD, NRI and NTI = Landscape + Patch size + Landscape \times Patch size). However, in these cases, we used parametric `ANCOVAs` instead of generalized linear models, after verifying that MPD, MNTD, NRI and NTI errors fit the normal distribution (Shapiro–Wilk test). All statistical tests were performed using JMP 8.0 (SAS Institute Inc., Cary, NC, USA).

Results

DIFFERENCES IN SPECIES DENSITY

Tree species density (species per 0.1 ha) was highly variable among patches, averaging 37 species (range = 4–64 species) in the sapling assemblage and 34 species (range = 13–48 species) in the adult assemblage (Table 1). Species density of saplings differed among landscapes (factor Landscape; $\chi^2 = 17.0$, $df = 2$, $P < 0.001$) and was significantly higher in IDL than in LDL and HDL (contrast tests, $P < 0.05$ in all cases) (Table 1; Fig. 2a). Species density of adults did not differ among landscapes ($\chi^2 = 1.48$, $df = 2$, $P = 0.48$; Fig. 2b). Species density was positively related to patch size (covariable Patch size) in both assemblages (saplings: $\chi^2 = 4.25$, $df = 1$, $P = 0.04$; adults: $\chi^2 = 4.83$, $df = 1$, $P = 0.03$), and the

Table 1. Species density (number of species/0.1 ha), stem density (stems/0.1 ha) and tree phylogenetic structure and diversity of tree assemblages (both saplings and adults) in 45 rain forest patches located in three landscapes of Los Tuxtlas, Mexico, with different deforestation levels*

	LDL			IDL			HDL		
	Mean (\pm SD)	Min	Max	Mean (\pm SD)	Min	Max	Mean (\pm SD)	Min	Max
Species density									
<i>Saplings</i>	36.4 (9.9)	17	51	45.5 (9.7)	29	64	28.9 (12.3)	4	51
<i>Adults</i>	34.3 (8.2)	13	43	37.1 (6.2)	25	48	31.5 (7.9)	16	41
Stem density									
<i>Saplings</i>	106.3 (40.2)	33	198	173.7 (48.1)	99	260	94.1 (44.3)	4	168
<i>Adults</i>	75.2 (28.2)	23	133	79.5 (15.2)	53	108	71.3 (15.4)	49	101
MPD									
<i>Saplings</i>	419.9 (44.6)	279.3	464.4	410.8 (33.6)	350.9	471.5	427.8 (49.7)	317.3	482
<i>Adults</i>	373.9 (39.3)	280.5	435.3	370.7 (28.7)	331.2	425.8	398.9 (40.3)	330.3	460.6
MNTD									
<i>Saplings</i>	136.6 (42.3)	88.8	249.3	135.7 (36.2)	99.7	221.4	157.8 (81.8)	82	354.2
<i>Adults</i>	118.9 (16.8)	96.5	145.5	118.2 (17.8)	93.7	151.8	113.8 (20.8)	76.4	158.5
NRI									
<i>Saplings</i>	-1.168 (0.6)	-2.260	-0.316	-0.629 (1.0)	-2.317	1.053	-1.491 (0.7)	-2.622	-0.107
<i>Adults</i>	0.221 (0.8)	-1.314	1.583	0.611 (0.8)	-1.033	1.847	-0.540 (1.0)	-2.112	1.490
NTI									
<i>Saplings</i>	-0.315 (1.4)	-4.177	1.232	-0.875 (1.3)	-4.129	0.723	-0.047 (1.1)	-2.109	1.863
<i>Adults</i>	0.333 (0.9)	-1.134	2.142	0.281 (0.8)	-1.304	1.271	0.826 (0.7)	-0.204	2.148

*LDL, lowest deforestation level, 24% of remaining forest cover; IDL, intermediate deforestation, 11%; HDL, highest deforestation, 4%. MPD, mean phylogenetic distance; MNPd, mean nearest taxon phylogenetic distance; NRI, net relatedness index; NTI, nearest taxon index.

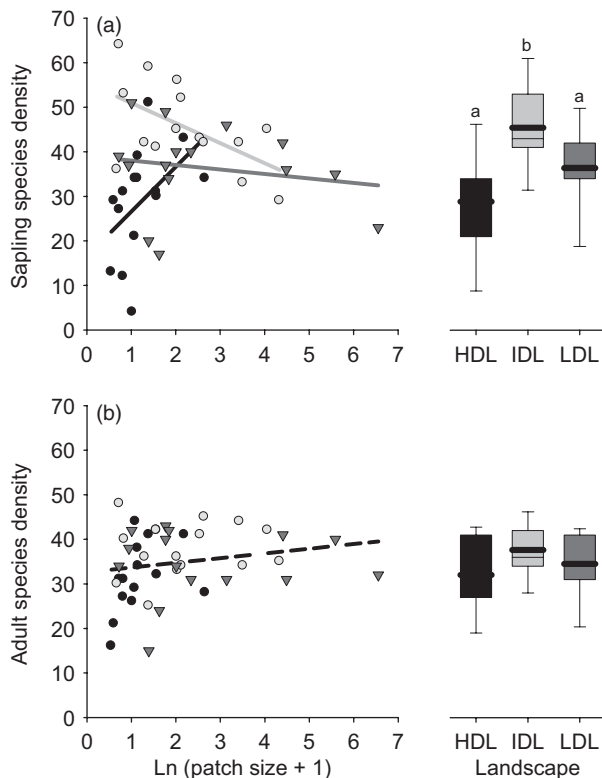


Fig. 2. Differences in tree species density among forest patches of different sizes and landscapes with different deforestation levels located in Los Tuxtlas, Mexico (LDL, lowest deforestation level; IDL, intermediate deforestation; HDL, highest deforestation). We indicate means (solid line), median (thin line), 25th and 75th percentiles (boundaries of boxes), and 10th and 90th percentiles (whiskers above and below box plots) for each landscape. Results are separately presented for sapling (a) and adult (b) tree assemblages. The landscapes that differed among each other are indicated with different letters (Tukey–Kramer HSD tests, $P < 0.05$). The between-species density and patch area relationships significantly differed among landscapes in the sapling assemblage (black line, HDL; light grey, IDL; dark grey, LDL), but not in the adult assemblage (the general linear relationship is indicated with a dotted line).

between-species density and patch area relationships (interacting factor, Landscape \times Patch size) significantly differed among landscapes in the sapling assemblage ($\chi^2 = 22.8$, $df = 2$, $P < 0.001$), but not in the adult assemblage ($\chi^2 = 3.6$, $df = 2$, $P = 0.17$). In particular, we found a positive slope in HDL, but negative or neutral slopes in IDL and LDL, respectively (Fig. 2a). Although the stem density of sapling assemblages was significantly higher in IDL than in HDL and LDL (Tables 1 and S2), after controlling for differences in stem density (i.e. rarefaction protocol), LDL accumulated significantly more species than IDL and HDL (see Fig. S1). Thus, differences in species density of saplings among landscapes do not appear to be related to differences in stem densities.

DIFFERENCES IN PHYLOGENETIC DIVERSITY AND STRUCTURE

Mean phylogenetic distance averaged 419.5 million years in the sapling assemblage and 381.2 million years in the adult

assemblage, but a large variation was observed among forest patches and landscapes (Table 1, Fig. 3a,b). MNTD also varied greatly among sites (Table 1, Fig. 3c,d), averaging 143.4 million years in the sapling assemblage and 117.0 million years in the adult assemblage. Net relatedness index (NRI) averaged -1.1 in the sapling assemblage and 0.1 in the adult assemblage. Finally, NTI averaged -0.4 in the sapling assemblage and 0.5 in the adult assemblage (Table 1).

Overall, MPD, MNTD, NRI and NTI were not affected by patch size and landscape forest cover (Table 2; Fig. 4). Only NRI differed among landscapes (factor Landscape) when considering the sapling assemblage (Table 2), being significantly lower in IDL than in LDL and HDL (Fig. 4a). Nonetheless, the explanatory power of the whole model was too low (R^2 adj = 0.11 , $P = 0.09$).

Considering the adult assemblage, eight of the 45 forest patches (18%) showed significantly non-random phylogenetic structure with respect to the regional species pool: six were clumped and two were phylogenetically even. For these eight forest patches, which were distributed across the three landscapes, we detected 38 of 435 internal nodes that had more or less descendent taxa than expected by chance (see Table S3). Nodes involved a wide range of major clades of the angiosperm phylogeny, from magnoliids to monocots and eudicots, as well as many lower clades, such as families and genera (e.g. Annonaceae, Lauraceae, Moraceae, *Croton*, *Inga*, *Ficus*). No 'sigless' or 'sigmore' occurred in more than three of the eight plots (Table S3), indicating that differences in phylogenetic structure from plot to plot were caused by many unrelated taxa.

Considering the sapling assemblages, 13 forest patches were significantly more even than expected, relative to random assemblages drawn from the regional phylogeny. For those plots with non-random phylogenetic structure, 33 of 425 internal nodes presented fewer or more descendent taxa than expected by the null model (Table S3). Eudicots had fewer species in 11 of the 13 plots, while palms (Arecaceae), Monimiaceae and the major clade of magnoliids had more species in five, six and four plots, respectively. The other 28 nodes did not occur in more than three plots, suggesting that the differences among plots in the phylogenetic structure of sapling assemblages also relied on many distantly related taxa.

Discussion

Our results show that in strongly deforested and fragmented rain forests, differences in tree species density among forest patches and landscapes result in few and very weak differences in the phylogenetic diversity and structure of remaining tree assemblages. This finding indicates that local extirpation of tree species in forest patches may occur randomly or uniformly (but not in a clustered manner) throughout the phylogenetic tree (Fig. 1b). Similarly, Santos *et al.* (2010) find that local extirpation of tree species in small (< 80 ha) forest patches does not affect significantly the phylogenetic structure and diversity of remaining tree assemblages in the severely

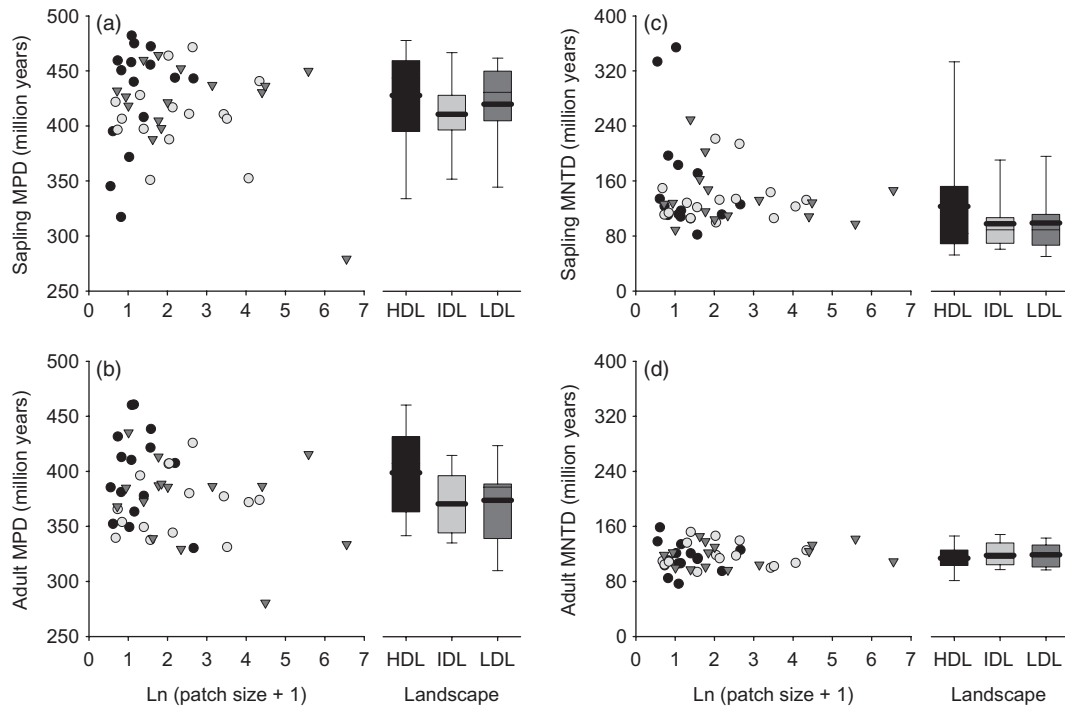


Fig. 3. Differences in mean phylogenetic distance (MPD) and mean nearest taxon phylogenetic distance (MNTD) among forest patches of different sizes and landscapes with different deforestation levels located in Los Tuxtlas, Mexico (LDL, lowest deforestation level; IDL, intermediate deforestation; HDL, highest deforestation). We indicate means (solid line), 25th and 75th percentiles (boundaries of boxes), and 10th and 90th percentiles (whiskers above and below box plots) for each landscape. Results are separately presented for sapling (a, c) and adult (b, d) tree assemblages.

Table 2. Effects of landscapes with different deforestation levels and patches of different sizes on tree phylogenetic diversity in Los Tuxtlas, Mexico

Phylogenetic metric	Whole model		Analyses of Covariance		
	R^2 adj	F	Landscape	Patch size	Landscape \times Patch size
Mean phylogenetic distance (MPD)					
Sapling assemblage [†]	0.04	1.35 ^{n.s.}	1.95 ^{n.s.}	0.96 ^{n.s.}	2.36 ^{n.s.}
Adult assemblage [‡]	0.05	1.47 ^{n.s.}	0.58 ^{n.s.}	0.49 ^{n.s.}	0.65 ^{n.s.}
Mean nearest taxon phylogenetic distance (MNTD)					
Sapling assemblage	0.01	1.08 ^{n.s.}	0.25 ^{n.s.}	2.93 ^{n.s.}	1.61 ^{n.s.}
Adult assemblage	-0.09	0.27 ^{n.s.}	0.38 ^{n.s.}	0.17 ^{n.s.}	0.35 ^{n.s.}
Net relatedness index (NRI)					
Sapling assemblage	0.11	2.10 ^{n.s.}	4.62*	1.53 ^{n.s.}	0.57 ^{n.s.}
Adult assemblage	0.22	3.42*	1.45 ^{n.s.}	2.48 ^{n.s.}	1.07 ^{n.s.}
Nearest taxon index (NTI)					
Sapling assemblage	-0.01	0.96 ^{n.s.}	1.53 ^{n.s.}	0.96 ^{n.s.}	0.11 ^{n.s.}
Adult assemblage	-0.00	0.99 ^{n.s.}	0.63 ^{n.s.}	0.14 ^{n.s.}	0.22 ^{n.s.}

We indicate F values and the significance level (^{n.s.} $P > 0.05$; * $P < 0.05$).

[†]Trees with dbh ranging from 2.5 to 10 cm.

[‡]Trees with dbh > 10 cm.

fragmented Brazilian Atlantic rain forest. Thus, although some life history traits in Neotropical (Chazdon *et al.* 2003) and temperate (Willis *et al.* 2010) plants are phylogenetically conserved, the traits that confer vulnerability to tropical tree species in fragmented landscapes (e.g. seed size, shade tolerance, regeneration niche, pollination and sexual systems; Laurance *et al.* 2006; Santos *et al.* 2008; Lopes *et al.* 2009) seem to be

phylogenetically convergent. Consistent with this hypothesis, Girão *et al.* (2007) and Lopes *et al.* (2009) show that in the Brazilian Atlantic rain forest, most tree reproductive traits are not phylogenetically conserved. For instance, the species pollinated by vertebrates belong to 5 families, 4 orders and 4 superordinal clades, and the species pollinated by small insects belong to 19 families, 13 orders and 8 superordinal clades. Sim-

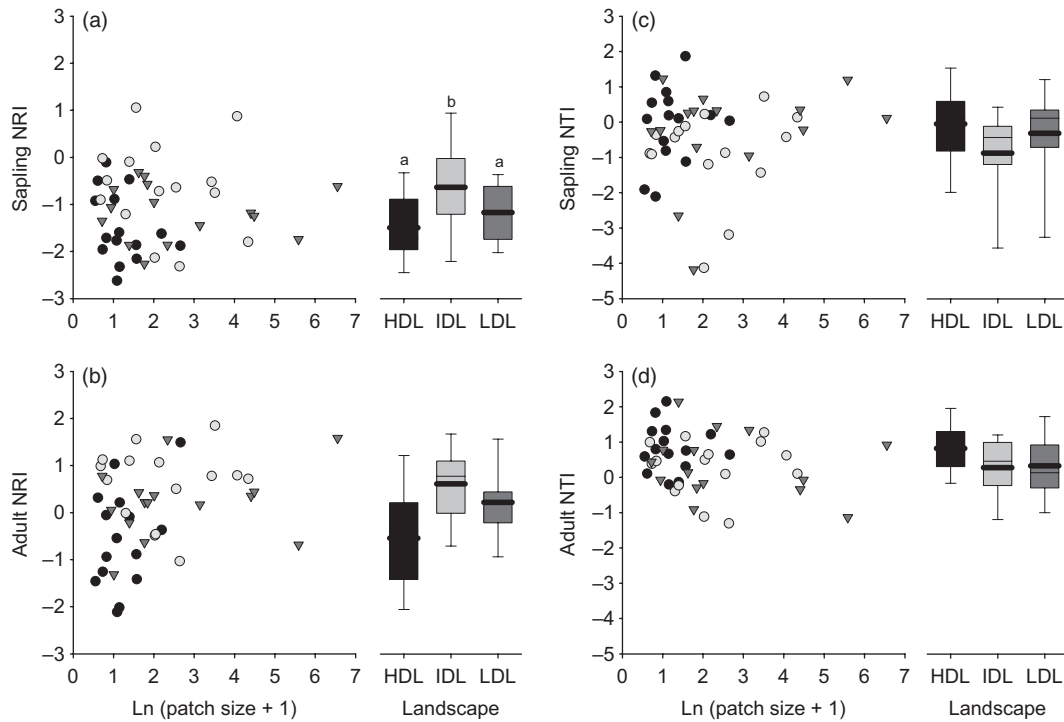


Fig. 4. Differences in net relatedness index (NRI) and nearest taxon index (NTI) among forest patches of different sizes and landscapes with different deforestation levels located in Los Tuxtlas, Mexico (LDL, lowest deforestation level; IDL, intermediate deforestation; HDL, highest deforestation). We indicate means (solid line), median (thin line), 25th and 75th percentiles (boundaries of boxes), and 10th and 90th percentiles (whiskers above and below box plots) for each landscape. Results are separately presented for sapling (a, c) and adult (b, d) tree assemblages. The landscapes that differed among each other are indicated with different letters (Tukey–Kramer HSD tests, $P < 0.05$).

ilarly, Santos *et al.* (2010) demonstrate that tree phylogenetic diversity and structure are not correlated with the proportion of species within different tree functional groups (i.e. shade-tolerant, large-seeded and emergent tree species). Nevertheless, the phylogenetic distribution of these traits remains to be properly described, and further studies are necessary to accurately assess the phylogenetic conservatism of the traits that confer vulnerability to extinction in fragmented forests.

Despite the fact that species density increased with patch size, particularly in the landscape with the highest deforestation level (HDL), MPD and MNTD were not related to patch size in any landscape. Given that light-demanding pioneer tree species can become dominant in either young (< 50 year old) or ageing small forest patches (e.g. Laurance *et al.* 2006; Santos *et al.* 2008; Tabarelli *et al.* 2010), and species richness and abundance of large-seeded zoochorous tree species may be lower in forest patches and along forest edges (Melo, Dirzo & Tabarelli 2006; Melo *et al.* 2010), the probability of sampling two conspecific individuals could increase with decreasing patch size, resulting in a positive relationship between MPD and patch size. The lack of such a relationship in our data set could be explained by the fact that in our study sites the proportion of animal-dispersed species is independent of both patch size and the remaining forest cover in the landscape (Arroyo-Rodríguez *et al.* 2009a). Also, pioneer tree species do not proliferate in Los Tuxtlas as they do in the Central Amazonia and the Brazilian

Atlantic forest (Arroyo-Rodríguez *et al.* 2009a). Apparently, as has been found for other tropical landscapes of The Mexican Transition Zone (Rös, Escobar & Halffter 2011), the complex biogeographical history of Los Tuxtlas associated with elevated volcanic activity, hurricanes and proximity to the temperate region resulted in a regional species pool that is more tolerant to the environmental changes in forest patches than those of South American tropical rain forests, where disturbance has been less frequent and intense (see Corlett & Primack 2006 for more details on cross-continental differences of tropical forests).

The negative relationship between species density and MNTD in the adult assemblage is not surprising, because as more species are excluded from the local assemblage, the remaining species will be more distantly related to at least one of the already-sampled species (see Vamosi *et al.* 2009). The lack of such a relationship in the sapling assemblage may be related to the fact that, in contrast to the sapling assemblage, the adult assemblage is less dynamic in ecological and phylogenetic terms (Letcher 2010). However, in hyperdynamic regenerating assemblages, in which many processes can affect the establishment, growth and survival of plant species (see Chazdon 2008; Letcher 2010), MNTD may vary with species density in a less predictable fashion. This complexity in processes affecting the organization of sapling assemblages may explain why we failed to detect the negative relationship we observed for the adult assemblages. Nonetheless, regardless of the assemblage considered, the differences in MNTD across

landscapes were very weak, indicating a regional maintenance in phylogenetic distance between pairs of co-occurring saplings or adults belonging to different taxa.

The phylogenetic structure of sapling and adult assemblages also differed slightly across landscapes. When it differed significantly, as in the NRI of adult assemblages, there was an increase in the overall level of phylogenetic evenness in smaller forest patches, indicating that forest fragmentation is filtering out individuals and species within various clades but not entire lineages (see Fig. 1b). This finding is supported by the fact that many unrelated taxa significantly contribute to the non-random phylogenetic structure of adult and sapling assemblages (Table S3). Thus, in contrast with other studies demonstrating that phylogenetic conservatism of some functional traits can cause phylogenetic clustering along environmental gradients in temperate forests (e.g. Cavender-Bares, Keen & Miles 2006; Willis *et al.* 2010), these findings also suggest low phylogenetic conservatism of the traits that underlie susceptibility to forest fragmentation in the tropics.

IMPLICATIONS FOR CONSERVATION

As rain forests are increasingly deforested and fragmented worldwide, tropical landscapes are increasingly dominated by very small forest patches and edge-affected habitats. This situation has fuelled a crucial debate about the prospect of biodiversity and ecosystem services in human-modified landscapes (Lindenmayer *et al.* 2008; Gardner *et al.* 2009; Isbell *et al.* 2011). Our results suggest that there is a low phylogenetic conservatism of traits associated with high vulnerability to forest fragmentation and have two basic conservation implications. First, although habitat fragmentation may impose important ecological barriers that negatively impact some tree functional groups (e.g. Laurance *et al.* 2006; Santos *et al.* 2008; Lopes *et al.* 2009), this ecological filtering does not result in dramatic differences in phylogenetic diversity or structure, at least within a certain range of species loss. Thus, in strongly deforested and fragmented landscapes, such as the Los Tuxtlas region, where only 10% of the original forest cover remains across the entire Biosphere Reserve (Dirzo & García 1992), it is critical to conserve as many rain forest patches as possible, because both large and small patches conserve most of the regional tree evolutionary history. This perspective clearly contrasts with that offered by those approaches based on species richness, from which human-modified landscapes tend to exhibit limited conservation value due to drastic reductions on the number of tree species from local (Santos *et al.* 2008) to regional levels (Lôbo *et al.* 2011).

Second, maintaining the phylogenetic diversity and structure of tree assemblages in fragmented rain forests may be critical for ecosystem function (reviewed by Cavender-Bares *et al.* 2009). For example, phylogenetic diversity predicts community productivity better than species richness (Cadotte, Cardinale & Oakley 2008) or functional group diversity (Cadotte *et al.* 2009). Furthermore, high phylogenetic diversity can promote ecosystem stability (M. W. Cadotte, R. Dinnage & D.

Tilman, unpublished work) by ensuring that sufficient ecological strategies are represented in an assemblage to ensure persistence of the ecosystem in the face of changing conditions (Cavender-Bares *et al.* 2009). In this sense, the fact that local species extirpation resulted in few and very weak differences in the phylogenetic diversity and structure of tree assemblages is a hopeful finding for the future of fragmented tropical rain forests, as it suggests that ecosystem functioning may be maintained despite the disappearance of some tree species. However, a major focus of future studies should be the identification of threshold values for species loss under which the phylogenetic diversity and structure can be drastically altered, potentially compromising the ecosystem functioning of fragmented landscapes, as well as the evolution of tropical floras and associated plant consumers in these emerging and already dominant environments. This approach, in addition to disentangling the relationships between phylogenetic diversity and functional diversity of tropical tree assemblages, will have practical value for conservation planning and strategies.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Differences in sapling species density among landscapes after controlling for differences in stem density (rarefaction).

Table S1. Accuracy of tree inventory.

Table S2. Differences in stem density among forest patches and landscapes.

Table S3. Clades contributing to non-random phylogenetic structure (NODESIC procedure).

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