Received: 23 November 2021 | Accepted: 3 May 2022

DOI: 10.1111/1365-2664.14197

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Forest loss and treeless matrices cause the functional impoverishment of sapling communities in old-growth forest patches across tropical regions

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Funding information
Consejo Nacional de Ciencia y Tecnología, Grant/Award Number: 863752 and SEP-CONACyT scholarship 2015-253946; Netherlands Organization for Scientific Research, Grant/Award Number: 863.15.017; Interdisciplinary Research and Education Fund of Wageningen University; PAPIIT-UNAM, Grant/Award Number: IN201020

Handling Editor: Nubia Carla Santos Marques

Abstract

1. Landscape-level disturbances, such as forest loss, can profoundly alter the functional composition and diversity of biotic assemblages. In fact, the landscape-moderated functional trait selection (LMFTS) hypothesis states that landscape-level disturbances may act as environmental filters that select a set of species with disturbance-adapted attributes while causing the loss of species with disturbance-sensitive attributes, ultimately compromising ecosystem functioning. However, the impact of landscape patterns on the functional composition and diversity of tropical regenerating trees (saplings) is unknown.
2. Using a multiscale approach to identify the best spatial scale (i.e. the scale of effect), we tested the effect of forest cover, matrix openness and forest patch density (fragmentation) on functional composition and functional diversity of tree saplings in old-growth forest patches ($n = 59$) in three Mexican rainforest regions with different degree of deforestation. For 368 species and ~23,000 individuals, we compiled information from global and national databases on six functional traits related to seed dispersal and plant establishment and calculated their community abundance-weighted mean (CWM) and three complementary functional diversity indices.
3. Forest loss and matrix openness reduced functional richness and evenness, but only in the two most deforested regions. Overall, fragmentation had contrasting effects on functional diversity and composition, but correlated negatively with some functional traits in the most deforested region. Importantly, in the regions with high-to-intermediate degree of deforestation, functional composition experienced major changes: maximum height, seed mass, fruit size and wood density decreased, and SLA increased, in forest patches surrounded by open matrices in highly deforested and fragmented landscapes. This caused a shift of community traits towards more disturbed-adapted attributes.

4. *Synthesis and applications*. In agreement with the LMFTS hypothesis, our results confirm that landscape modifications in regions undergoing high and long-lasting deforestation greatly impoverish the functional composition and diversity of sapling communities. The shift from communities composed mainly by conservative attributes towards communities with a higher prevalence of disturbance-adapted attributes disrupts the future community structure and jeopardizes critical ecosystem functions. Management practices focused on preventing deforestation, increasing forest cover and promoting treed matrices are necessary to preserve the functionality of these species rich but increasingly threatened rainforests.

KEYWORDS
disturbance-sensitive attributes, ecosystem services, fragmentation per se, landscape management, landscape structure, matrix quality, sapling assembly, seed dispersal traits

1 | INTRODUCTION

Deforestation and forest degradation are major drivers of the current biodiversity crisis, particularly threatening species-rich ecosystems such as tropical rainforests (Gibson et al., 2011). Increasing evidence demonstrates the negative impact of forest loss on plant taxonomic diversity (Newbold et al., 2016; Watling et al., 2020) and on important ecological processes, such as seed dispersal (San-José et al., 2020) and tree regeneration (Arasa-Gisbert, Arroyo-Rodríguez, Galán-Acedo, et al., 2021). Yet, very few studies have evaluated the effects of forest loss and other landscape changes on plant functional diversity and functional trait composition (Zambrano et al., 2019). Improving our understanding of plant functional responses to landscape changes is critical because the loss of functional diversity and shifts in community functional properties can result in the loss of key ecosystem functions and associated ecosystem services (Díaz et al., 2007; Pan et al., 2016).

Functional diversity quantifies the distribution of functional units in a multidimensional space (Villéger et al., 2008). It is also an umbrella concept that groups a myriad of different, and sometimes overlapping, functional diversity indices (Mouchet et al., 2010). In an attempt to simplify this conceptual complexity, Mason et al. (2005) proposed three orthogonal indices of functional diversity: functional richness, evenness and divergence. The scarce evidence from tropical forests (Zambrano et al., 2019) suggests that each of these indices may be affected by landscape structural changes in different ways. In particular, Rocha-Santos et al. (2020) demonstrated that landscape-level forest loss has negative impacts on plant functional richness, positive effects on functional divergence and no effects on functional evenness. However, their study focused on adult trees in a single rainforest region. Therefore, additional studies focusing on other life stages and considering multiple regions with varying degree of deforestation are needed to better understand the relative effects of landscape changes on functional diversity.

The above issue is not trivial, as the effects of forest spatial configuration, such as forest fragmentation, on the attributes of biological assemblages have been hypothesized to depend on the regional deforestation context (Andrén, 1994; Villard & Metzger, 2014). For example, the 'fragmentation threshold hypothesis' predicts that the effects of fragmentation should be stronger in regions with very low (<30%) forest cover (Andrén, 1994; Lehtilä et al., 2020; Palmeirim et al., 2019). Other studies suggest that the strongest biological responses to fragmentation occur in regions with intermediate levels (30% to 50%) of forest cover (Pardini et al., 2010; Villard & Metzger, 2014). However, an increasing number of studies (e.g. Arasa-Gisbert, Arroyo-Rodríguez, Galán-Acedo, et al., 2021), including a meta-analysis with plants and animals (Watling et al., 2020), suggest that fragmentation effects are generally weak, independently of the regional context. However, as this issue is commonly assessed by considering changes in the number of species only, the effects of habitat fragmentation on the functional diversity and composition of biotic assemblages have been largely overlooked.

In theory, landscape changes can also affect the abundance and distribution of specific functional attributes. For example, the 'landscape-moderated functional trait selection hypothesis' (Tscharntke et al., 2012) states that landscape structure (i.e. composition and configuration) can pose an important filter selecting species according to their functional traits. In the case of trees, species with conservative trait values (e.g. hard-wooded, heavy-seeded species) are more vulnerable to disturbance and can experience a decrease in their populations in deforested landscapes, while species with acquisitive trait values (e.g. light-wooded, small-seeded species) may increase their populations in more deforested landscapes (Filgueiras et al., 2021; Tabarelli et al., 2012). For example, increased resource availability (i.e. more light, water and space) inside forest patches in highly deforested landscapes can favour the growth and survival of plant species with high specific leaf area, low wood density and small seeds (Poorter et al., 2008, 2019). By contrast, these conditions can negatively affect the growth and survival of heavy-seeded, hard-wooded and softer-leaved conservative species (Berenguer et al., 2018; Poorter et al., 2008, 2019; Rocha-Santos et al., 2017). Recruitment of heavy-seeded, large-fruited and animal-dispersed species may also be particularly negatively affected in highly deforested landscapes because the greater distances between fragments and the decline of seed dispersers can hinder seed dispersal across the landscape (Benchimol et al., 2017; Peres et al., 2016). Nevertheless, the effects of landscape-scale variables on plant functional diversity and functional traits have been poorly studied (see Zambrano et al., 2019), and to our knowledge, no study to date has specifically focused on seedlings and saplings.

Here, we evaluated the relative effects of landscape composition (i.e. forest cover and matrix openness) and configuration (i.e. patch density and forest edge density) on functional diversity and functional trait composition of sapling communities in old-growth tropical forest fragments. We also explore if such effects vary across three regions with different degrees of deforestation to assess whether landscape configuration effects are stronger or milder under certain regional contexts. We focused on the sapling community because plants at this stage are seemingly more sensitive to current landscape changes than adult trees (Benchimol et al., 2017). Furthermore, the future composition and structure of forest communities can be better predicted by exploring changes in composition at the early life cycle stages (Berenguer et al., 2018).

We predicted reductions in functional richness and evenness in forest fragments surrounded by landscapes with lower forest cover and matrices with lower tree cover (Rocha-Santos et al., 2020). In contrast, we predicted relatively weak responses to landscape configuration variables (see Fahrig, 2017), although following the 'fragmentation threshold hypothesis', these responses could be stronger in regions with very low (< 30% of forest cover; Andrén, 1994) or intermediate (30%–50%; Villard & Metzger, 2014) degrees of deforestation. Finally, in accordance with the 'landscape-moderated functional trait selection hypothesis' (Tscharntke et al., 2012), we predicted landscape modifications to act as a filter capable of selecting species with disturbance-adapted functional trait values and excluding species with functional trait values sensitive to such changes (e.g. species with heavy seeds or high wood density).

2 | MATERIALS AND METHODS

2.1 | Study regions and sampling design

We studied old-growth forest patches in three tropical humid fragmented regions from south-eastern Mexico with different deforestation patterns and land-use history: Marqués de Comillas (low-deforestation region), Los Tuxtlas (intermediate-deforestation region) and Northern Chiapas (high-deforestation region) (Figure 1). General characteristics of each studied region are detailed in Table 1 and Appendix S1.

We selected old-growth forests because of their irreplaceable value for biodiversity conservation (Barlow et al., 2007; Gibson et al., 2011). Although secondary forests can also be valuable for restoring some ecosystem functions and biodiversity, such value can vary considerably among secondary forests (see Chazdon et al., 2009, 2016), and the recovery of species composition in secondary forests can take centuries (see Rozendaal et al., 2019). Therefore, we focused our study on the effects of landscape changes on functional properties in old-growth forest patches, which retain most of the original adult tree species composition.

In each region, we selected 20 old-growth forest patches (i.e. 60 forest patches in total). The patches varied in size from 2.3 to 129 ha, except for two bigger patches, a 640-ha patch in IDR, and another patch of 3,410 ha in LDR (see Figure 1). We applied a non-random sampling; instead, patch selection was based on the following criteria. First, they had to be located at least 1,500 m apart from each other to increase between-sample independence (Eigenbrod et al., 2011). Second, forest patches should have similar edaphic, topographic and altitudinal characteristics (< 600 m a.s.l.). Third, they should have few or no signs of human disturbance (e.g. stumps, human trails, etc.). Finally, the forest patches should be embedded in landscapes with different structure (e.g. contrasting percentages of forest cover at the same spatial scale) to increase as much as possible the variation in all explanatory landscape variables, and thus increase our ability to detect significant diversity-landscape relationships (Eigenbrod et al., 2011). Time since deforestation varied between regions (~20 years difference, see Table 1) but we can consider that the selected forest patches within each region were created in similar times because regional deforestation occurred very intensively over short periods (e.g. ~30% of old-growth forest cover was deforested in only 10 years in the low-deforestation region; Carabias et al., 2015).

Sampling was conducted in the dry season, from January to May 2018. At the centre of each forest patch, we established 25 circular plots of 1.60 m radius ($8\,m^2$ each, which represents $200\,m^2$ sampled in each patch), in a grid of 5×5 plots with a 30 m separation between them. In each plot, all saplings (excluding palms and lianas) ≥ 30 cm in height and < 1 cm of diameter at breast height (DBH) were identified and counted. Then, we summed up the values obtained for the 25 plots to obtain a single value for each forest patch (i.e. sampling unit). In-situ identification was made by experts on tropical plant identification with over 30 years of expertise. Species not identified in the field were collected for identification at the National Herbarium of Mexico (MEXU, Mexico City) and vouchers were deposited in this collection. We followed the nomenclature of the Missouri Botanical Garden electronic database (available at http://www.tropicos.org). This research was conducted in accordance with the legal requirements of the National Autonomous University of Mexico (UNAM), and the country of Mexico. All study patches are private lands, and we were granted access to the study sites by local communities and landowners. As we only collected some parts (e.g. stems and leaves) of plant specimens, and no species was threatened, we did not require any permit from the Secretary of Environment and Natural Resources (SEMARNAT) of Mexico. This study also did not require ethical approval.

2.2 | Functional traits

We recorded 23,846 saplings belonging to 69 families, 212 genera and 415 woody species (Arasa-Gisbert, Arroyo-Rodríguez,

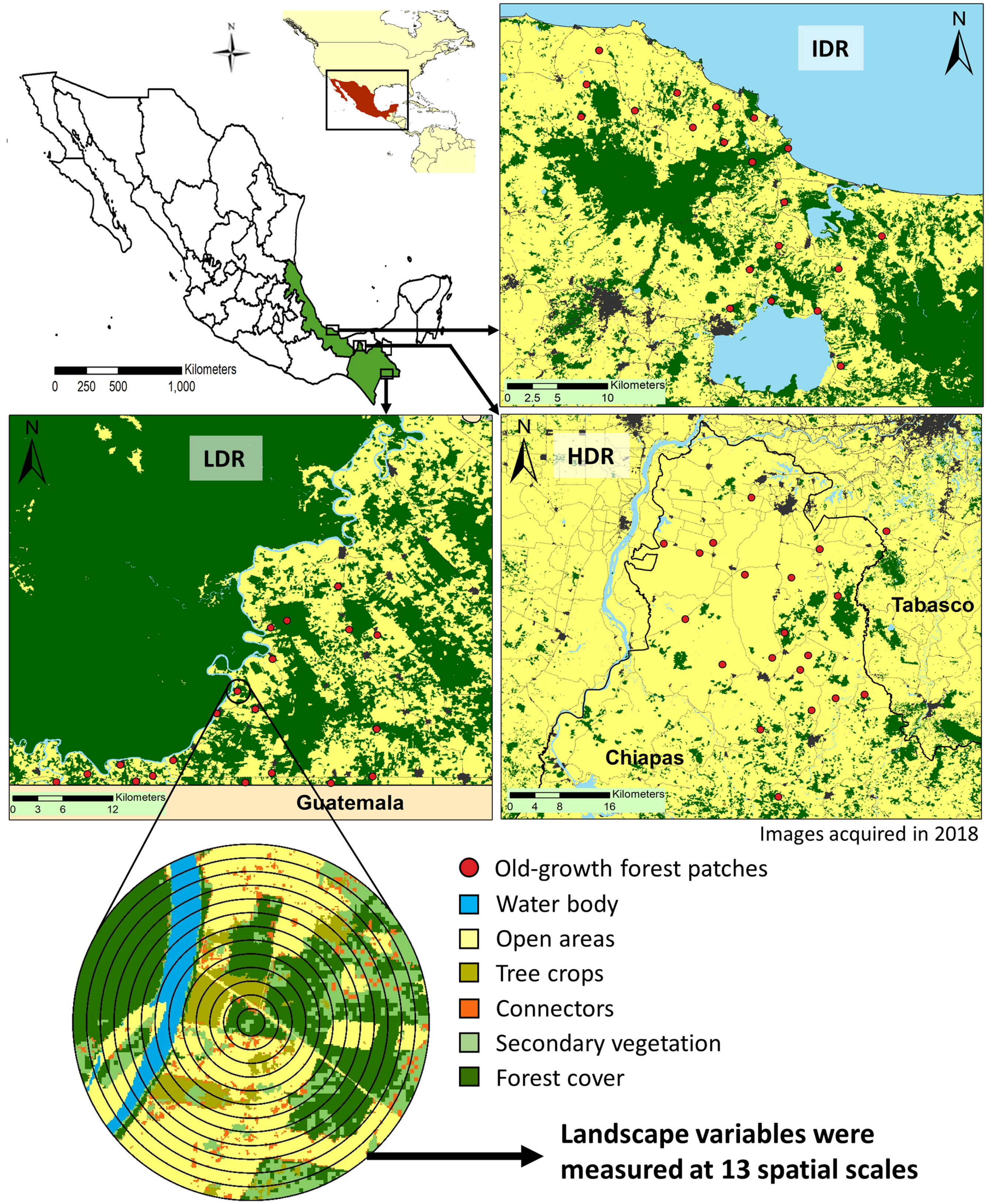

FIGURE 1 Location of the 60 old-growth forest patches included in this study (red dots) in three tropical regions of the southeast of Mexico: Marqués de Comillas (LDR), Los Tuxtlas (IDR) and Northern Chiapas (HDR). Old-growth forests are shown in green, anthropic matrices (e.g. secondary forests, cattle pastures, annual crops) in light yellow, water bodies in light blue and human settlements in dark grey. We also show one of this forest patches in detail, including the 13 concentric spatial scales (i.e. buffers) used to extract the landscape variables (indicated by different colours in the legend)

TABLE 1 General information about the three studied tropical regions in south-eastern Mexico

Variable	Marqués de Comillas (LDR)	Los Tuxtlas (IDR)	Northern Chiapas (HDR)
Location	16°19′–16°2′N; 91°6′–90°41′W	18°68′–18°38′N; 95°24′–94°96′W	17°87′–17°42′N; 93°33′–93°00′W
Mean annual temperature (°C)	24–26[1]	24–25[2]	25–26[2]
Annual precipitation (mm)	3,000–3,500[1]	3,500–4,500[2]	2,500–3,500[2]
Land-use history (years)	~40[1]	~60[3]	~70[4]
Matrix composition	Heterogeneous[1]	Cattle pastures[3]	Cattle pastures[4]
Remaining old-growth forest cover in the region (%)	~36%[1]	~19.7%[5]	~5%[4]
Mean forest patch size (ha)[a]	27.46 ± 32.91 (129–2.4)	26.86 ± 26.60 (97–2.5)	19.59 ± 28.99 (113–2.3)
Forest cover (%)[b]	35.42 ± 23.79 (100–10.32)	32.33 ± 19.52 (88.55–10.63)	16.30 ± 16.91 (63.78–1.86)
Open areas in the matrix (%)[b]	58.11 ± 24.40 (0.0–85.78)	72.23 ± 11.84 (43.11–89.72)	61.30 ± 22.37 (0.37–89.58)
Patch density (n/ha)[b]	0.16 ± 0.10 (0.01–0.38)	0.43 ± 0.24 (0.10–0.94)	0.09 ± 0.11 (0.01–0.40)
Edge density (m/ha)[b]	87.76 ± 30.89 (0.0–130.58)	118.20 ± 37.61 (46.71–195.75)	49.31 ± 25.95 (8.06–89.54)

References: [1]Carabias et al., (2015), [2]CLImate COMputing (http://clicom-mex.cicese.mx), [3]Laborde et al. (2011), [4]Anzures-Dadda and Manson (2007), [5]Von Thaden et al. (2020).

[a] We indicate the mean (±*SD*) values and range (in parenthesis) of the forest patch sizes considered in this study. For this calculation we excluded one forest patch in LDR (3,410 ha) and another one in IDR (640 ha) that were selected to increase the forest cover range in the 13 scales considered.

[b] We indicate the mean (±*SD*) values and range (in parenthesis) of each landscape metric used in this study. These values correspond to the landscape metrics measured in a concentric landscape (i.e. buffer) of 700-m radius (the central radius of the 13 considered radii) from the centre of each sampling site.

TABLE 2 Functional traits and their related functional attributes (min. – max.). We show the percentage of the species for which information for each functional trait was recorded (% All). For these species, we also show the percentage of the species whose functional trait information was obtained at the species (% Sp.), genus (% Gen.) or family (% Fam.) level. Fruit size (diameter): 1, < 5 mm; 2, 5–14.9 mm; 3, 15–29.9 mm; 4, 30–49.9 mm; 5, > 50 mm

Functional traits	% All	% Sp.	% Gen.	% Fam.	Functional attribute range
Maximum tree height	99.7	100	0	0	2–70 m
Seed mass	91.7	40.3	39.4	0.9	0.04–13,000 mg
SLA	82.5	58.2	41.8	0	4.28–65.19 mm^2/mg
Wood density	95.4	45.5	45.9	8.6	0.16–1.20 g/cm^3
Fruit size	99.7	100	0	0	Very small fruit (1), small fruit (2), medium-sized fruit (3), large fruit (4), very large fruit (5)
Dispersal syndrome	97.6	100	0	0	Zoochory, Anemochory, Barochory, Autochory

Ortiz-Díaz, et al., 2021). For this set, we excluded 47 species: 36 morphospecies, 7 exotic species and 4 species for which we could not obtain functional data. Therefore, we were able to obtain information on functional traits from the literature for 368 species, which summed 22,848 individuals. We collected six functional traits that represent the whole plant trait economic spectrum (Díaz et al., 2016), play a key role in plant regeneration (Poorter et al., 2008) and are sensitive to environmental modifications (Pinho et al., 2021, Appendix S2): tree maximum height (Hmax, m), seed mass (SM, mg), specific leaf area (SLA, mm^2/mg), fruit size (FS, mm), wood density (WD, g/cm^3) and dispersal syndrome (Table 2).

We compiled information of the functional traits mostly from global or national databases. Specifically, we used the 'Seed Information Database' (Royal Botanic Gardens Kew, 2021) to obtain data for SM, the 'TRY Plant Trait Database' (Kattge et al., 2020) for SLA values and 'the Global Wood Density Database' (Zanne et al., 2009) for WD values. For Hmax and FS we used mainly the information included in Ibarra-Manríquez and Cornejo (2010), although we were unable to obtain specific values of these traits for each region. We used additional sources (e.g. Moles et al., 2005) to increase the information available for the afore-mentioned functional traits.

For those species for which we could not find the functional attributes for some trait, we calculated the mean of the functional trait at the genus or family level (Table 2). We did this for highly phylogenetically conserved traits only, such as SM (Moles et al., 2005;

TABLE 3 Community abundance-weighted mean (CWM ± *SD*) of each functional trait and functional index for each of the three study regions: low-deforestation region (LDR), intermediate-deforestation region (IDR) and high-deforestation region (HDR). Statistically significant differences between regions are indicated with different letters next to the values, while the absence of letters indicates no significant differences between regions. One-way ANOVAs were conducted to assess the significance of between-region differences

Trait/Functional index	LDR	IDR	HDR
Maximum tree height (m)	19.18 ± 3.3	19.03 ± 4.4	16.97 ± 2.5
Seed mass (mg)	382.3 ± 151	523.6 ± 270	413.13 ± 186
SLA (mm^2/mg)	19.25 ± 0.98 (a)	17.54 ± 1.8 (b)	18.18 ± 1.03 (b)
Fruit size (1 to 5)	2.44 ± 0.19	2.5 ± 0.3	2.6 ± 0.4
Wood density (g/cm^3)	0.60 ± 0.042	0.56 ± 0.05	0.59 ± 0.042
Dispersal syndrome (cat.)	Zoo	Zoo	Zoo
Functional Richness (0 to 1)	0.23 ± 0.1 (a)	0.097 ± 0.1 (b)	0.16 ± 0.06 (c)
Functional Evenness (0 to 1)	0.66 ± 0.046	0.69 ± 0.05	0.66 ± 0.07
Functional Divergence (0 to 1)	0.78 ± 0.037	0.76 ± 0.08	0.72 ± 0.11

Norden et al., 2009), WD (Chave et al., 2006) and, to a lesser extent, SLA (Flores et al., 2014). This is a common procedure (e.g. Pinho et al., 2021) that has been strongly recommended (see Chave et al., 2006), especially in tropical forests, where the information on such traits for most tropical tree species remains scarce (Cornwell et al., 2019). By doing so, we gathered trait values for at least 80% of the total abundance of each community (i.e. forest patches), which is required for community functional properties to be representative (see Pakeman & Quested, 2007). Only for one forest patch we could not meet this standard and it was excluded from the analyses. Additionally, some SM values sourced by the literature corresponded to the seed fresh weight. To standardize the data, we used the following equation to transform fresh weight to dry weight: dry weight = $(0.921 \times \text{fresh weight})^{0.9407}$ (Moles et al., 2004).

2.3 | Functional diversity indices

We used three complementary indices of functional diversity: functional richness (FRic), functional evenness (FEve) and functional divergence (FDiv; Mason et al., 2005; Villéger et al., 2008). FRic represents the amount of functional space occupied by the community (Villéger et al., 2008), and is based on the convex hull concept, which is the minimum convex hull that includes all species considered. FEve represents the homogeneity in the distribution of species trait abundances of a community, so FEve decreases when species trait abundances are distributed less uniformly among the included species or when functional distances among species are less regular (Mouchet et al., 2010; Villéger et al., 2008). Finally, FDiv measures how far the abundances of the different species are from the centre of the functional space (Villéger et al., 2008).

2.4 | Landscape variables

We estimated four landscape metrics: two metrics of landscape composition (forest cover and matrix openness) and two metrics of landscape configuration (forest patch density and forest edge density). We selected these landscape variables because of their ecological importance, the expected strong influence of them on sapling functional diversity and composition, and their widespread use in landscape studies (see Fahrig, 2017). Landscape variables were assessed in 13 concentric landscapes (i.e. buffers or landscape areas) of 100- to 1,300-m radius (at 100-m intervals) from the centre of each sampling site using ArcGis 10.5 software and the Patch Analyst extension (Rempel et al., 2012). This multiscale approach was used in order to identify the spatial scale at which the relationship between each response variable and each landscape metric is strongest (i.e. scale of effect; Jackson & Fahrig, 2015). In this regard, it is worth noting that at the 100-m radius, the concentric buffer usually encompasses only the surface of the focal patch, resulting in low spatial variability; thus, considering scales smaller than 100-m radius is unlikely to add variability to the explanatory variables. Forest cover was estimated by dividing the total amount of old-growth forest area in the landscape by the landscape area × 100 (%). Matrix openness was calculated as the percentage of the matrix covered by open areas (i.e. cattle pastures, annual crops, water bodies and human settlements). This means that the complement of the values concerning matrix openness correspond to the values of treed matrix (i.e. secondary forests, tree plantations and connectors). Patch density is a frequently used measure of fragmentation (Fahrig, 2017) and was calculated as the number of old-growth forest patches in the landscape divided by the landscape area (*n*/ha). Edge density was estimated as the length of the perimeter of all old-growth forest patches in the landscape divided by the landscape area (m/ha).

2.5 | Data analyses

We examined the effect of landscape metrics on functional composition using the community abundance-weighted mean (CWM), which weights the species' trait values by their relative abundances and represents the trait value of a randomly selected individual in the community (Pinho et al., 2021). To calculate the CWM for dispersal syndrome, which is a categorical variable, we converted each class (e.g. zoochory) to a binary variable. We calculated CWM trait values using the function 'functcomp' present in the FD package (Laliberté et al., 2014). To explore the effects of landscape metrics on functional diversity we used the three indices of functional diversity mentioned above: FRic, FEve and FDiv. These three functional indices were calculated by including all species (372) and the six functional traits (Table 2) with the function 'dbFD' present in the FD package (Laliberté et al., 2014) in R (R Core Team, 2016). We log-transformed SM and Hmax in order to meet the assumption of normality. We also assessed the potential effects of two environmental variables (i.e. mean annual temperature and annual precipitation) on each functional variable within each region, but as most relationships were non-significant (Table S1), we did not include environmental variables as covariates in the statistical models that are described below.

Once we obtained the response variables (i.e. CWMs and functional diversity indices) for each community ($n = 59$), we calculated the scale of effect of each landscape metric (i.e. forest cover, matrix openness, patch density and edge density). To this end, we fitted generalized linear models (GLMs) between each landscape metric and each response variable for each region and spatial scale. The scale of effect has been emphatically recommended because multiscale landscape studies are often conducted at suboptimal scales, which can cause the species-landscape relationship to go undetected when it actually exists (see Jackson & Fahrig, 2015). Overall, we fitted 1,248 models (3 regions × 4 landscape metrics × 8 response variables × 13 spatial scales). All models were evaluated with Gaussian distribution error, as all response variables included in the final analyses were continuous. For each model we calculated the percentage of explained deviance (pseudo-R^2) as a measure of the goodness-of-fit of the model (Crawley, 2007). For each landscape metric, the spatial scale with the highest pseudo-R^2 among the 13 scales considered (i.e. the scale of effect) was selected for subsequent analyses (Table S2).

For each region, we used GLMs with all four-landscape metrics (each one measured at its respective scale of effect) to assess the relative importance of each landscape metric in predicting each response variable. We calculated the variance inflation factor (VIF) for each model to detect multicollinearity among landscape metrics using the CAR package from R version 3.0.1 (Fox et al., 2012). A significant collinearity between forest cover and edge density (VIF > 4) was detected in the high-deforestation region, so we removed edge density from subsequent analyses in all regions.

We used an information-theoretic approach and multi-model inference to assess the relative effect of the examined landscape metrics on each response variable (Burnham & Anderson, 2002). For each response variable (i.e. CWMs and functional diversity indices) we constructed eight models that represented all possible combinations of the three landscape variables and the null model. We calculated the sample-corrected Akaike information criterion (AICc) for each model. Then, we ranked the models according to their AICc, from the lowest AICc (the best-supported model) to the highest AICc (the least-supported model) (Table S3). Thereafter, we summed the Akaike weights ($\sum w_i$) of each landscape metric included in the models, as this summed value indicates the probability that a landscape metric would be included in the best fitting model if the data were collected under the same circumstances. Thus, Akaike weights can be interpreted as the relative importance of each landscape metric on each response variable (Burnham & Anderson, 2002; Giam & Olden, 2016). We considered a landscape metric to have important effects on a given response if the following three criteria were met simultaneously: (a) the model-averaged unconditional variance was lower than the model-averaged parameter estimate (Burnham & Anderson, 2002; Table S4); (b) it showed a relatively high sum of Akaike weights ($\sum w_i$); and (c) the model in which the landscape variable was included had a relatively high percentage of explained deviance (Crawley, 2007). All models and calculations were conducted under the GLMULTI package for R version 3.3.2 (Calcagno & de Mazancourt, 2010).

3 | RESULTS

The regions showed similar functional diversity and composition values (Table 3). Only functional richness (FRic, $F = 15.9$, $p < 0.001$) and SLA ($F = 8.8$, $p < 0.001$) were higher in the low-deforestation region than in the other two regions (Table 3).

3.1 | Effects of landscape variables on functional diversity

We found that the scale of effect of each landscape variable on each response did not differ significantly among regions ($F = 1.87$, $p = 0.16$) or among response variables ($F = 0.90$, $p = 0.51$). Yet, the effects of landscape metrics on functional diversity differed between regions (Figure 2a). Overall, landscape structure had stronger effects (i.e. higher pseudo-R^2) on functional diversity in the high-deforestation region than in the other two regions. The effects of landscape metrics on FRic were generally weak (cf. the relatively low pseudo-R^2 and/or Akaike weights in Figure 2), but it was strongly and negatively associated with matrix openness in the high-deforestation region. FEve was positively related to forest cover in all regions and negatively associated with matrix openness in intermediate- to high-deforestation regions; however, these two landscape variables showed weak effects on FEve in the low-deforestation region. Patch density showed strong negative effects on FEve in the high-deforestation region, but such effect was contrary and less strong in the other two regions. FDiv was negatively related to forest cover and matrix openness in the intermediate-deforestation region, and to a lesser extent, in the high-deforestation region. FDiv was also strongly and positively associated with matrix openness in the low-deforestation region. Patch density showed strong and positive effects on FDiv in the high-deforestation region and, to a lesser extent, in the intermediate-deforestation region. In contrast, patch density had strong and negative effects on FDiv in the low-deforestation region.

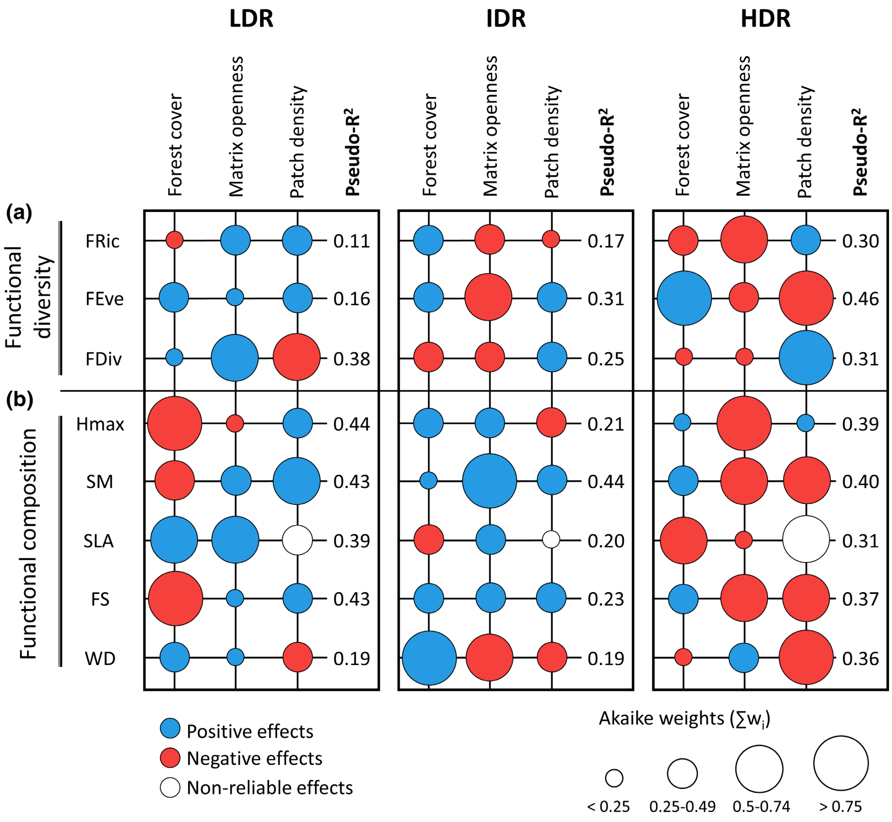

FIGURE 2 Effect of the composition and configuration landscape metrics (columns) on (a) functional diversity and (b) functional composition (rows) of the sapling community in the three study regions: low-deforestation region (LDR), intermediate-deforestation region (IDR) and high-deforestation region (HDR). The size of the circles represents the sum of the Akaike weights ($\sum w_i$), which show the importance of each landscape metric on each response variable. Blue and red circles indicate positive or negative effects respectively. Note that, in the case of SLA, positive effects (blue colour) must be interpreted as negatives for the community (and vice versa for negative effects), because higher SLA values are typical of disturbance-adapted species. Circles without colour indicate that the unconditional variance was higher than the parameter value, which means that the sum of the Akaike weights for that landscape metric is not accurate and may include zero. We also show the pseudo-R^2, which is the percentage of explained deviance for each model. FRic, Functional Richness; FEve, Functional Evenness; FDiv, Functional Divergence; Hmax, Maximum tree height; SM, Seed Mass; SLA, Specific Leaf Area; FS, Fruit Size; WD, Wood Density

3.2 | Effects of landscape variables on functional composition

Similar to functional diversity, the effects of landscape metrics on functional composition (i.e. CWMs) differed considerably among regions (Figure 2b). In the low-deforestation region, forest cover had strong negative effects on Hmax, SM and FS, and positively ones on SLA. In the same region, matrix openness had positive effects on SLA and SM, while patch density had positive effects on Hmax, SM and FS and a negative effect on WD. In the intermediate-deforestation region, forest cover had positive effects on most functional traits except SLA, with WD showing the most important and positive association with forest cover. Similarly, matrix openness had positive effects on most functional traits except for WD. By contrast, patch density had weak effects on most functional traits in the region; this landscape metric only showed important and positive associations with SM. In the high-deforestation region, forest cover was importantly and positively related to SM and FS, and negatively to SLA, while matrix openness had strong and negative effects on almost all functional traits. Similarly, patch density had strong negative effects on SM, FS and WD.

Finally, we observed a decrease in the abundance of species with conservative traits caused by all landscape metrics in the two most deforested regions (Figure 3). Specifically, the proportion of tall species, with large fruits, heavy seeds or high wood density decreased in landscapes with lower forest cover (Figure 3a) and/or higher matrix openness (Figure 3b) in one or both regions. The effects of patch density were either positive or negative (Figure 3c). In contrast, in the low-deforestation region, forest loss and fragmentation increased the abundance of species with conservative traits, while no effects were observed for matrix openness (Figure S1).

4 | DISCUSSION

To our knowledge, this is the first assessment of the effects of landscape structure on functional properties of sapling communities across tropical rainforest regions with different deforestation

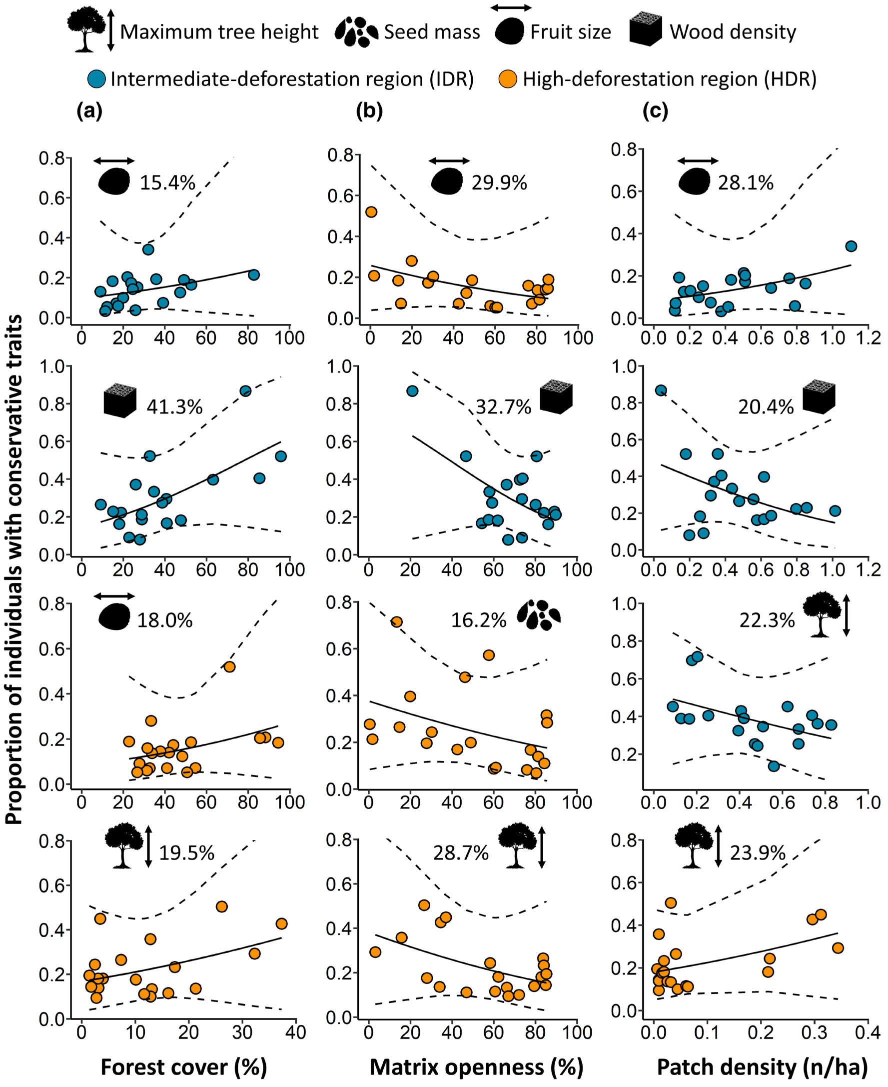

FIGURE 3 Relationship between the proportion of individuals with conservative traits (high stature: > 25 m; heavy seeds: > 500 mg; large fruits: > 30 mm; hard woods: > 0.675 g/cm^3) over the total number of individuals for each region and landscape metrics. Only relationships with $R^2 > 0.15$ are shown. The black line shows the predicted estimates from the binomial regression using a generalized linear model and the area enclosed by the two dashed lines represents the 95% confidence interval. Coloured points indicate the forest patches

level. In particular, we found that, as predicted, forest loss and matrix openness had negative effects on functional diversity and altered the community functional composition in regions with intermediate to high deforestation. Importantly, as predicted by the landscape-moderated functional trait selection hypothesis (Tscharntke et al., 2012), all functional traits (maximum tree height, seed mass, specific leaf area, fruit size and wood density) in the two most deforested regions were negatively affected by at least one landscape variable, particularly favouring the persistence of acquisitive functional attributes. However, landscape changes in the low-deforestation region did not influence the community functional composition, suggesting that such a potential landscape-moderated environmental filtering is weak in relatively well-preserved regions (i.e. with high forest cover and heterogeneous matrices). The effect of patch density (i.e. forest fragmentation) depended on the response variable, with either positive or negative effects. However, supporting the fragmentation threshold hypothesis (Andrén, 1994), fragmentation effects tended to be stronger and negative in the most deforested region. Finally, we did not find any pattern regarding the scale of the effect, a result that contrasts with those from a previous study on sapling taxonomic diversity (Arasa-Gisbert, Arroyo-Rodríguez, Galán-Acedo, et al., 2021). As discussed below, our findings have critical ecological and applied implications, especially regarding the functional impoverishment of forest patches in highly deforested regions.

Our results suggest that forest loss and the expansion of treeless areas in the anthropogenic matrix are the main factors reducing sapling functional diversity in highly deforested landscapes. Forest loss and matrix openness negatively affected functional richness and functional evenness in intermediate- to high-deforestation regions. This finding supports previous studies demonstrating the detrimental effects of forest loss (Lôbo et al., 2011; Rocha-Santos et al., 2017, 2020) and matrix openness (Carneiro et al., 2016; Laliberté et al., 2010; Zambrano et al., 2020) on functional diversity of adult tropical tree communities, and could be related to three non-exclusive mechanisms. First, the lack of adult trees in more deforested landscapes with treeless matrices can limit fruit and seed availability (i.e. seed source limitation; Clark et al., 1998). Second, these landscape changes can also reduce the abundance and/or species richness of seed dispersers (Carrara et al., 2015; Garmendia et al., 2013), and constrain their dispersal movements across the landscape (Tucker et al., 2018), potentially causing seed dispersal limitation (Howe & Smallwood, 1982). Finally, forest loss and matrix openness could also change the environmental conditions within forest patches (e.g. the increase in forest temperature; Arroyo-Rodríguez, Saldaña-Vázquez et al., 2017), making them unsuitable for seed germination and seedling and sapling survival (i.e. establishment limitation; Howe & Smallwood, 1982). Taken together, these three mechanisms can reduce the functional richness and evenness of sapling communities because they can have stronger negative impacts on some functional trait values (e.g. species with large fruits and heavy seeds). Additionally, other mechanisms not evaluated in this study (e.g. landscape-level resilience) may also influence sapling functional diversity (López et al., 2017). Regardless of the underlying mechanism, the loss of extreme or rare functional attributes may ultimately reduce the amount of functional space occupied by the community.

The loss of functional diversity was accompanied by the alteration of the community traits in the most deforested regions. In at least one of the two most deforested regions, forest loss, matrix openness or fragmentation had negative effects on typical functional attributes of old-growth forest species (i.e. conservative attributes, see Pinho et al., 2021) such as larger seed mass, larger fruit size, higher wood density, lower specific leaf area and higher maximum height. Therefore, our results support the 'landscape-moderated functional trait selection hypothesis' (Tscharntke et al., 2012), since landscape changes are negatively impacting species with functional attributes more sensitive to landscape changes, while favouring species with a particular set of functional attributes that make them more resistant to those changes. This is consistent with what has been observed in adult trees of the Brazilian Atlantic Forest (Lôbo et al., 2011; Magnago et al., 2014; Rocha-Santos et al., 2017). In particular, the increasing predominance of short-statured, light-wooded, light-seeded and small fruited sapling species in our highly deforested regions (Figure 3 and Table S5) indicates that generalist and pioneer species are proliferating.

The shift of sapling community traits towards more disturbed-adapted attributes in intermediate- to high-deforestation regions could compromise the future physiognomy and functionality of these forest patches. For example, forest loss and matrix openness in the most strongly deforested regions decreased the proportion of tall-statured, hard-wooded and soft-leaved sapling species. In tropical forests, such species correlate positively with high biomass productivity (Finegan et al., 2015; Prado-Junior et al., 2016) and carbon storage (Cavanaugh et al., 2014; Ruiz-Jaen & Potvin, 2011), and participate in key role ecosystem functions and processes such as water and climate regulation or fire and erosion prevention (reviewed by de Bello et al., 2010). Thus, forest loss and matrix openness could jeopardize fundamental ecosystem functions and services within forest patches in the next decades as saplings grow to adult stages—an interesting avenue for future research.

Interestingly, we observed relatively weak effects of landscape patterns on functional diversity and composition of sapling communities in the low-deforestation region. We hypothesize that this finding could be related to the relatively high spatial heterogeneity in this region. The remaining forest cover (35% of the landscape area) is distributed among a large number of different-sized patches embedded in a highly heterogeneous matrix, which included different treed covers. Landscapes with this structure are known to be of high value for biodiversity conservation, as they cannot only promote species coexistence and prevent species extinction but also enhance landscape connectivity and forest regeneration (reviewed by Arroyo-Rodríguez et al., 2020; Melo et al., 2013). In fact, these landscape features can favour the coexistence of both forest specialist and habitat generalist species (Pardini et al., 2010), thus favouring the presence of species with different functional attributes across the region.

Finally, we found that fragmentation effects (i.e. patch density) were relatively stronger in the most deforested region (< 10% forest cover). This supports the 'fragmentation threshold hypothesis' (Andrén, 1994). Lehtilä et al. (2020) also found that fragmentation effects on boreal forests of Sweden are stronger in landscapes with < 25% of forest cover, and Palmeirim et al. (2019) found that fragmentation thresholds on small tropical mammals can be smaller (i.e. < 10% forest cover). This can be associated with the fact that patches located in heavily deforested regions are typically smaller and more exposed to edge effects than patches located in regions with high forest cover. Thus, a higher incidence of edge effects can have higher effects of fragmentation on functional diversity and certain edge-sensitive functional traits, such as fruit size, seed mass or wood density (Magnago et al., 2014; Zambrano et al., 2020). However, as this is a community-level study, more studies would be necessary to identify those species more vulnerable to fragmentation in highly deforested regions.

5 | CONCLUSIONS

Our findings suggest that sapling communities in forest patches located in highly deforested landscapes surrounded by treeless matrices are decreasing their functional richness and evenness, especially in tropical regions with intermediate to high degree of deforestation. Specifically, we found that saplings of canopy species with hard woods and leaves, and bearing large fruits and seeds, seem to be more vulnerable to landscape changes and tend to be gradually disappearing in the most deforested regions. It is important to mention that we did not account for intraspecific variability of functional traits among regions and landscapes. However, the large set of species assessed ($S = 368$) and the strong negative responses of some functional attributes to landscape changes suggest that accounting for intraspecific variability would not modify the overall results. Therefore, to prevent the potential consequences that these community changes could have for ecosystem functioning (e.g. seed dispersal, carbon storage) and services (e.g. forest regeneration, carbon sequestration), we need to implement biodiversity-friendly management practices in human-modified landscapes (sensu Arroyo-Rodríguez et al., 2020).

In particular, we can propose some general management actions based on our findings. First, to prevent the negative impact of forest loss and matrix openness on functional richness and evenness of sapling communities, we (1) should stop deforestation and (2) increase as much forest cover as possible, especially in highly tropical deforested regions. The novel contribution here is that by preventing forest loss, we are not only preventing the loss of species (reviewed by Arroyo-Rodríguez et al., 2020), but also the loss of valuable functional attributes. The conservation effectiveness of this management strategy will be optimized if combined with an adequate management of the anthropogenic matrix. In particular, our findings highlight the importance of (3) preventing open areas in the matrix, which can be carried out by combining crops with native trees (i.e. the so-called 'agroforestry systems'), or delimiting the lands with live fences composed of native trees. These two general principles (i.e. preventing forest loss and increasing tree cover in the matrix) increase the availability of fruits and seeds of native trees in the landscapes and can also favour seed dispersal and sapling recruitment of both forest specialist and habitat generalist species (reviewed by Arroyo-Rodríguez, Melo, et al., 2017), thus contributing to maintain high levels of functional diversity and the original functional attributes (i.e. conservative attributes) in these forest patches. However, this does not mean that disturbance-adapted attributes typical of pioneer and generalist species are not valuable for conservation. The dominance of these attributes in highly deforested landscapes can also contribute to restoring some ecosystem functions and services. For instance, there is evidence that some disturbance-adapted species or genera found in our study sites (e.g. *Leucaena leucocephala*, *Acacia* sp., *Enterolobium* sp.) re-established the nutrient cycling process and carbon sequestration in tropical degraded lands in Brazil (Macedo et al., 2008). Also, the small-seeded, light-wooded pioneer species *Ochroma pyramidale* can prevent bracken fern invasion in fragmented tropical forests of Mexico (Douterlungne et al., 2013). Therefore, an optimal spatial scenario to guide conservation action could be one like the Marqués de Comillas region, with ~35% forest cover in a large number of different-sized patches embedded in a highly heterogeneous matrix. Our findings suggest that this scenario can preserve the functional diversity and composition of saplings independently of the landscape context, and closely resembles the one proposed by Arroyo-Rodríguez et al. (2020) as an optimal spatial design to preserve forest species in human-modified landscapes.

ACKNOWLEDGEMENTS

We appreciate the financial support provided by SEP-CONACyT (scholarship 2015-253946). R.A.-G. obtained a PhD scholarship from CONACyT, Mexico. M.L. was supported by research program ALW (863.15.017), financed by the Netherlands Organization for Scientific Research (NWO) and by the Interdisciplinary Research and Education Fund of Wageningen University (INREF) as part of the FOREFRONT program. M.M.-R. received financial support from PAPIIT-UNAM (grant IN201020). Gilberto Jamangapé and Santiago Sinaca provided field assistance and helped with species identification. We thank the landowners of the Marqués de Comillas, Los Tuxtlas and Northern Chiapas regions for granting access to their properties. We gratefully thank three anonymous reviewers for their valuable suggestions to a previous version of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

R.A.-G. and V.A.-R. conceived the research idea, with advice from J.A.M., M.M.-R. and M.L.; R.A.-G. collected the field data and compiled information on functional traits; R.A.-G. and V.A.-R. designed the methodology with advice from M.L.; R.A.-G. wrote the manuscript with feedback from V.A.-R., J.A.M., M.M.-R. and M.L. All authors contributed critically to the drafts and gave final approval for submission. Our study was conceived and conducted, and the data collected, by authors based in the country where the study was carried out. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.gxd2547pg (Arasa-Gisbert et al., 2022).

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How to cite this article: Arasa-Gisbert, R., Arroyo-Rodríguez, V., Meave, J. A., Martínez-Ramos, M. & Lohbeck, M. (2022). Forest loss and treeless matrices cause the functional impoverishment of sapling communities in old-growth forest patches across tropical regions. *Journal of Applied Ecology*, 00, 1–14. https://doi.org/10.1111/1365-2664.14197