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Agricultural land-use diversity and forest regeneration potential in human- modified tropical landscapes

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ABSTRACT

A major challenge in tropical human-modified landscapes (HMLs) is meeting the ever-growing demand for agricultural products while conserving biodiversity and ecosystem services provided by forest ecosystems. Within this challenge, a major issue is the understanding of the forest potential to naturally regenerate in abandoned agricultural fields. To assess such potential, it is necessary to know the diversity of agricultural land uses in the landscape, quantify the ecological disturbance inflicted by such uses, and evaluate forest regeneration as a function of disturbance both at the field and landscape levels. Our previous work has shown that in abandoned fields the abundance and species diversity of regenerating rain forest trees decline as disturbance level increases. Here we aimed to achieve the following: 1) to quantify the diversity of agricultural land uses in HMLs; 2) to assess ecological disturbance regimes caused by different agricultural land uses, at the field and landscape scales; and 3) to identify groups of agricultural land uses with contrasting effects for forest regeneration at the landscape level. We approach these issues by using a case study of HMLs in a southeastern region of Mexico, which are representative of landscapes in the agricultural frontier in the Neotropics. We interviewed 68 landowners to gather information on agricultural land uses and management of 156 fields. Based on this information, we quantified an ecological disturbance regime associated with each field considering the following: field size (in hectares), duration of agricultural use (in years), and land-use disturbance severity (i.e. frequency or magnitude of fire, agrochemicals, machinery, grazing or removal of tree cover). By integrating disturbance inflicted by different land uses and the proportion of the landscape covered by each land use, we constructed a landscape ecological disturbance index. Finally, by using this index and data gathered from nine landscapes (3×3 km each), we tested the hypothesis that structural attributes (abundance, biomass, and species diversity of trees) of regenerating forests decrease as agriculture disturbances increase in the landscape. There was a high inequality in the proportion of land allocated to the 13 recorded agricultural land uses, with cattle pastures representing *ca.* 90% of total agricultural land. There was a wide disturbance gradient, ranging from land uses with high (e.g. cattle pastures) to low disturbance (e.g. coffee and cocoa plantations). Three major groups of land uses with contrasting disturbance regimes were detected: 1) agroforestry systems, characterized by small size, low to intermediate duration, and low disturbance severity; 2) monocultures, typically small size, long duration, and medium to high disturbance severity; and 3) extensive farming, large size, short to intermediate duration, and high disturbance severity. Biomass and species diversity of regenerating forests consistently reduced with increasing levels of agriculture disturbance in the landscape. We conclude that positive balances between biodiversity conservation and agricultural production in HMLs will depend on establishing agricultural land uses that inflict low disturbance regimes (such as agroforestry systems) embedded in a matrix of old-growth forest and long-lasting second-growth forests. Our results may inform farmers, policy makers and land managers about HMLs where agricultural production and conservation of biodiversity and ecosystem services can be conciliated.

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1. Introduction

Beyond harboring the major biodiversity on Earth, tropical rain forests play a paramount role in human societies by providing critical goods and ecosystem services (Gibson et al., 2011). These forests, however, have experienced strong deforestation and degradation mostly because of forest conversion to agriculture (Geist and Lambin, 2002; Quezada et al., 2014). The major challenge in tropical land management is meeting the ever-growing demand for agricultural products while conserving biodiversity and enhancing rural livelihoods (DeFries et al., 2007; Harvey et al., 2008; Phalan et al., 2011).

Tropical rain forest conversion to agriculture on a large scale is a relatively recent phenomenon (Geist and Lambin, 2002). Contemporary human colonization of areas formerly covered by old-growth forests started a few decades ago, especially in the Neotropics (Lepers et al., 2005). Currently, it is increasingly common to find human-modified landscape (HMLs) composed of mosaics of different agricultural land uses, remnants of old-growth forests, patches of second-growth forests, and degraded lands (Chazdon, 2014). With the advance of the agricultural frontier, not only forest tends to disappear, but the forest regeneration potential may also decline under the effect of different agricultural land uses (Chazdon, 2014). Therefore, to meet the conservation of biodiversity, goods and services of tropical forest ecosystems with agricultural production, besides preserving old-growth forest remnants, one must find agricultural land uses that are friendly to forest regeneration.

It has been recognized that agroforestry and traditional smallholder agricultural land uses contribute to biodiversity conservation in HMLs, especially when land uses retain abundant tree cover that provides complementary habitats, resources, and connectivity for native biota (DeFries et al., 2007; Harvey et al., 2008). In the tropics, however, there is a wide array of agricultural land uses, and their impact on forest regeneration potential, once a field is abandoned, is poorly known (Melo et al., 2013; Zermeño-Hernández et al., 2015). In this context, a first step for exploring agriculture land uses which are friendly to biodiversity conservation is to quantify the diversity of agricultural land uses in the landscape, assess the ecological disturbance regimes imposed by such uses, and evaluate the impact of these disturbance regimes on forest regeneration potential (Zermeño-Hernández et al., 2015). Because in recent times there has been a global trend of land abandonment in the tropics (Cramer et al., 2008; Aide et al., 2013), this issue is of wide relevance.

In this paper, we aim to quantify the diversity of agricultural land uses, assess their associated ecological disturbance regimes, and evaluate effects of such regimes on forest regeneration potential at the field and landscape level. We based this analysis on an ecological disturbance index (EDI) we developed elsewhere with information provided by farmers and landowners (Zermeño-Hernández et al., 2015). We have shown that EDI is an inexpensive, quickly and efficiently predictor of forest regeneration potential at the field scale; we proved that plant density, richness, and species diversity of regenerating forest trees decrease exponentially as EDI increases. Here we expand our analysis to the landscape scale by assessing how structural attributes of second-growth forests change along landscapes differing in diversity of agricultural land uses and, therefore, in disturbance regimes. We used a study case in the Marqués de Comillas region, southeastern Mexico, where the old-growth forest to agriculture conversion resulted in the loss of 40% of old-growth forest in just 20 years (1976–1996, De Jong et al., 2000). This fast conversion dynamics has occurred in several HMLs found in the agro-forest frontier (*i.e.* those forested areas under recent conversion to agriculture) in the Neotropics as documented by Houghton (1994) and Lambin et al. (2003). Specifically, we ask the following questions: How diverse are the agricultural land uses in tropical HMLs undergoing forest conversion to agriculture? Which ecological disturbance regimes are inflicted by these agricultural land uses? Can these uses be classified according to their disturbance regime? What is the potential for forest regeneration in landscapes with contrasting levels of agriculture disturbance? Finally, we offer recommendations for farmers, landscape managers and policy makers that can promote positive balances between biodiversity conservation and agricultural production in HMLs.

2. Methods

2.1. Study area

The study was conducted in the region known as Marqués de Comillas (16° 7′4.01"N, 90°55′27.01"W), southeastern Mexico (Fig. 1).The climate is warm and humid, with a mean annual rainfall of about 3000 mm and a mean annual temperature of 23° C (Martínez-Ramos et al., 2009). The primary vegetation is tropical rain forest varying in structure and composition across different geomorphological units (Siebe et al., 1996).

Marqués de Comillas has undergone an extensive process of land-use change and forest loss (De Jong et al., 2000). Deforestation had an important boost during the 70 s of the past century when the Mexican government opened the region to colonization and provided subsidies for cattle ranching, as was also the case for other regions in México (Challenger and Soberón, 2008) and other countries (e.g. Walker et al., 2000). Deforestation continued during the 80s, fostered by the country's economic crisis, population growth and a deepening of rural poverty (Barbier and Burgess, 1996; Mendoza and Dirzo, 1999). This led to a highly modified and complex agricultural landscape, where crop fields, cattle pastures, patches of secondary forests and old-growth forest remnants are intermixed. The relatively recent land-use history in the study area provides the opportunity to compile land-use information directly from stakeholders.

2.2. Agricultural land-use characterization and associated ecological disturbance regimes

To characterize diversity of agricultural land uses in the landscape, we conducted 68 semi-structured interviews (corresponding to 156 agricultural fields) with landowners of three villages: Chajul (27 interviews), Loma Bonita (26) and Playón de la Gloria (15). The first village has 398 inhabitants and an area of 4840 ha, the second 164 inhabitants and 1731 ha, and the third 209 inhabitants and 1740 ha (INEGI, 2010). Thereafter, we considered these territories as different landscapes. With the interviews, we gathered information about type (*e.g.*, cattle pasture, cornfield, chili, fruit orchard), field size (hectares under a specific land use), duration (number of years under a specific land use) and disturbance severity (harshness of land-use practices considering fire incidence, agrochemical and machinery use, grazing intensity, and remaining tree cover in the field) of the agricultural use (Table 1) for each of the 156 studied fields. In addition, we inquired to each landowner how much area (in hectares) maintains covered by old-growth forest or secondary forest. Based on this data, for each landscape and for all landscapes combined, we quantify the diversity of agricultural land uses and the proportion of the landscape covered by each land use; see below.

To quantify disturbance regimes imposed by different agricultural land uses at the local field scale, we used the ecological disturbance index (EDI) developed by Zermeño-Hernández et al. (2015). This index incorporates, in an additive way, three major disturbance components (Pickett and White, 1985): size, duration

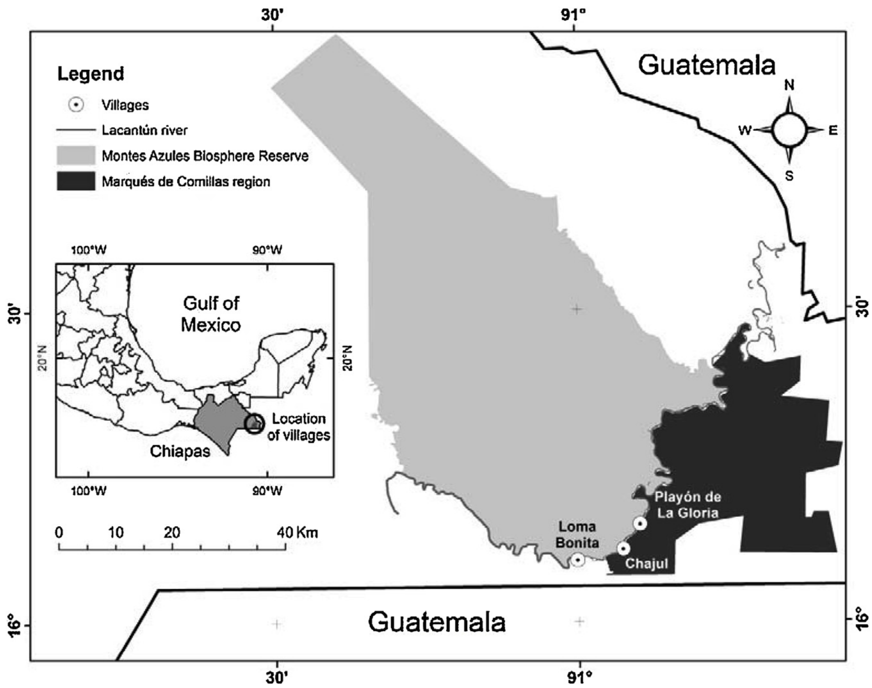

Fig. 1. Geographical location of the study area. Chajul, Loma Bonita and Playón de la Gloria villages are adjacent to Montes Azules Biosphere Reserve in the Marqués de Comillas municipality (dark area).

and disturbance severity, which were quantified as described in the supplementary material (A.1). This index varies from 0 to 3, with 3 being the maximum disturbance value; see details in Zermeño-Hernández et al. (2015). Additionally, we assigned a disturbance value of 0 to the old-growth forest remnants and of 0.25 to the secondary forest patches present in the studied fields, considering that old-growth forest represents the undisturbed condition and secondary forests may attain important levels of biodiversity and biomass, as documented by other studies conducted in Marqués de Comillas (van Breugel et al., 2006; Norden et al., 2015). Old-growth forests are at least 500 years old, corresponding to the time when Lacandon people occupied neighboring areas (De Vos, 1980). In contrast, because of short fallow periods, secondary forests are usually less than 15 years old and rarely reach 25 years (van Breugel et al., 2006).

To assess ecological disturbance regimes and forest regeneration potential at the landscape level, we used a system of nine landscapes of 3 × 3 km each that differed in the percentage of land covered by of old-growth forest remnants (7–100%), second-growth forests (0–88%), and agricultural land uses (0–93%). These landscapes were directionally selected by identifying areas with contrasting land cover types (i.e. old-growth forest, secondary forests, and agricultural land uses) and by avoiding overlapping. For this purpose we used satellite SPOT-5 (March 2013, free of clouds) images (10-m resolution) and a geographic information system (SAGA GIS). Land cover types were classified using the variance of the texture as described by Willhauck et al. (2000) and Castillo-Santiago et al. (2010). The spectral values for land cover type were as follows: $6.37 \pm 2.05\ \mu m$ for old-growth forest, 12.64 ± 3.33 to $20.15 \pm 4.04\ \mu m$ for secondary forest, and $33.05 \pm 8.62\ \mu m$ for agricultural land uses. In each landscape, a central core of 1 × 1 km was delimited where 30 circular plots (15 m radius, 708 m^2) were established at random. In the field, we located these plots by using a Global Positioning System (GPS). In

Table 1
Characterization of the ecological disturbance imposed by different agricultural land uses by using the ecological disturbance index (EDI; Zermeño-Hernández et al., 2015) components for three landscapes and combining them at Marqués de Comillas, in southeastern Mexico. Each disturbance component (columns) and mean values (bold figures) for different landscapes are separated by slashes. NA = Land use not available in a landscape.

Land Use	Duration	Size	Disturbance severity				
	(years)	(ha)	Fire Incidence	Chemical Use	Machinery Use	Grazing Severity	Tree Cover
	Chajul/Loma Bonita/Playón de la Gloria/All landscapes (mean)						
Banana	15/NA/NA/**15.0**	0.3/NA/NA/**0.3**	0/NA/NA/**0**	2.0/NA/NA/**2.0**	0/NA/NA/**0**	–	25 – 50%
Bean	23/23/18/**21.3**	1.2/0.4/0.8/**0.8**	0.4/0.2/0.5/**0.4**	1.6/0.3/1.8/**1.2**	0.6/0/0.1/**0.2**	–	0 – 25%
Chili	15/4/7/**8.7**	0.8/0.6/1.4/**0.9**	0.4/0/0.7/**0.4**	3.8/8.5/10.7/**7.7**	3.8/8.5/10.7/**7.7**	–	0 – 25%
Cocoa	25/12/14/**17.0**	4.0/4.4/4.5/**4.3**	0/0.1/0/**0**	0/0/0/**0**	0/0/0/**0**	–	> 50%
Coffee	NA/4/25/**14.5**	NA/0.5/1.0/**0.8**	NA/0.3/0/**0.2**	NA/0/0/**0**	NA/0/0/**0**	–	> 50%
Corn/Bean	20/13/NA/**16.5**	0.8/1.0/NA/**0.9**	0.2/0/NA/**0.1**	2.0/1.5/NA/**1.8**	0.1/0/NA/**0**	–	0 – 25%
Cornfield	25/15/18/**19.3**	1.1/1.3/1.5/**1.3**	0.3/0.4/0.2/**0.3**	1.7/0.4/1.1/**1.1**	0.3/0/0.1/**0.1**	–	0 – 25%
Mahogany	11/NA/NA/**11**	6.0/NA/NA/**6.0**	0/NA/NA/**0**	0/NA/NA/**0**	0/NA/NA/**0**	–	> 50%
Oil Palm	1.3/NA/NA/**1.3**	8.7/NA/NA/**8.7**	0.3/NA/NA/**0.3**	5.0/NA/NA/**5.0**	0.3/NA/NA/**0.3**	–	25 – 50%
Orchard	NA/12/15/**13.5**	NA/0.9/0.3/**0.6**	NA/0.1/0.3/**0.2**	NA/0/2.0/**1.0**	NA/0/0/**0**	–	> 50%
Pasture	19/10/10/**13.0**	18/12.5/16.7/**15.7**	0.4/0.3/0.3/**0.3**	2.9/0.2/0.7/**1.3**	0/0/0/**0**	2.4/1.5/1.6/1.8	25 – 50%
Rice	NA/15/NA/**15.0**	NA/0.5/NA/**0.5**	NA/1.0/NA/**1.0**	NA/0/NA/**0**	NA/0/NA/**0**	–	0 – 25%
Vegetables	NA/NA/12/**12.0**	NA/NA/0.4/**0.4**	NA/NA/10/**10**	NA/NA/1.0/**1.0**	NA/NA/0.5/**0.5**	–	1 – 25%

each plot, all trees with a diameter at breast height (DBH) of $\geq$ 10 cm were recorded, identified and measured in DBH. Moreover, we assigned a land use (agricultural type, old-growth forest, or secondary forest) to each plot; informants provided us with the fallow age of secondary forests. This classification matched $\geq$ 75% with the classification of land cover types gathered from the satellite images and the GIS analysis.

2.3. Data analysis

2.3.1. Diversity of agricultural land uses

To quantify the number of agricultural land uses present in the study area, we obtained curves of the cumulative number of agricultural land uses as a function of the cumulative number of interviews for each village and for the three villages as a group. For this, we constructed a matrix with the agricultural land uses as columns and the interviews as rows and cells containing presence (1) absence (0) scores. We then used EstimateS v.8 (Colwell, 2009) to generate the cumulative curves. We assumed that the interviews covered the total of agricultural land uses practiced in the region when the curve reached an asymptote.

Agricultural land-use diversity was calculated using different indices commonly used in the ecological literature (Magurran, 2004): 1) Shannon index [$H' = -\sum pi^*\log(p_i)$, which gives more relevance to less frequent elements (*i.e*, agricultural land uses with low proportions of land cover)], 2) Shannon evenness [$E = H'/\log(S)$], which measures the heterogeneity among elements (with S as the number of different agricultural land uses); and 3) inverse Simpson index ($D = 1/\sum p_i^2$), which gives more weight to dominant elements (diversity of the landscape increases as the value of D increases). In all these indices, we considered p_i as the proportion of land covered by each agricultural land use; we calculated p_i for each village and for the three villages as a total. Finally, we computed the Gini index (Gastwirth, 1972) to assess the inequality in the proportion of land covered by the different agricultural land uses. The Gini index varies between zero (highest equality, with all agricultural land uses having the same proportion of landscape area) and 1 (maximal inequality, with only one existing agricultural land use).

2.3.2. Ecological disturbance regimes at the field level

Differences in size and duration of disturbance among agricultural land uses were assessed using one-way ANOVA; data were log-transformed when they did not meet normality according to Shapiro-Wilk tests. Because the values of disturbance severity and EDI are non-normal distributed variables, as they are bounded between 0 and 5 and 0 and 3, respectively, differences were assessed through ANOVA on ranks. In all the analyses, each village was considered as a replicate, and only agricultural land uses with disturbance values in at least two landscapes were included. The differences in size and duration among agricultural land uses were compared by a Fisher *post-hoc* test for pairwise comparisons, while for those of disturbance severity and EDI we used *t*-tests as indicated for bounded variables (Crawley, 1993). The significance level was adjusted to 0.05 for all tests applied. All statistical analyses were performed with the statistical package R version 3.1.0 (R-Core-Team-R, 2015).

2.3.3. Similarity in disturbance regimes among agricultural land uses

To identify agricultural land uses with similar disturbance regimes, we performed a principal component analysis (PCA) with the statistical package CANOCO v. 4.5. For this analysis, we constructed a matrix with the disturbance components (size, duration, and disturbance severity) as columns, the agricultural land uses as rows and the relative value (from 0 to 1) of each disturbance component in the cells. We extracted two principal components that explained the higher amount of variance and integrated them within a two-dimensional Euclidean graph.

2.3.4. Disturbance regimes and forest regeneration at the landscape level

To quantify disturbance regimes at the landscape level, we calculated an EDI weighted mean (EDI_{wm}) for each landscape and combined them. This index was calculated as $EDI_{wm} = \sum EDI_i^* p_i$, where p_i is the proportion of the landscape covered for the land use i, EDI_i is the value of the ecological disturbance index corresponding to the agricultural land use i, the old-growth remnants and the secondary forest patches, and $\sum$ indicates the sum of all the products between EDI_i and p_i. In the index we included old-growth forest remnants and secondary forest patches as two additional agricultural land uses to have an integral assessment of the status conservation of the landscapes. Finally, the EDI_{wm} values obtained for each landscape were scaled to 3, the maximum possible value of EDI, to have a final value between 0 and 1.

To assess the effects of agricultural disturbance regimes on forest regeneration at the landscape level, we used the data gathered from the nine 3 × 3 km landscapes described above. For each landscape, we calculated the corresponding EDI_{wm} value, and by using only plots covered by secondary forests, we calculated an average value of tree density, basal area, species density, and species diversity per plot. Finally, we regressed the mean values of each of these attributes against EDI_{wm}. Through a multiple linear regression analysis, we assessed whether EDI_{wm} effects on each one of the forest attributes were independent of secondary forest age, considering that structural attributes of second-growth forests increase with fallow age (Norden et al., 2015). Furthermore, landscapes with low EDI_{wm} (i.e. recently opened to agriculture) could have younger secondary forests, and thus lower structural attribute values than landscapes with high EDI_{wm}.

3. Results

3.1. Agricultural land uses' diversity

The cumulative curve of the number of agricultural land uses against the number of interviews reached an asymptote, indicating that our sampling effort was enough to represent the diversity of agricultural land uses in each landscape and in the three landscapes as a whole (Fig. A.1). The old-growth forest remnants covered 33% (691 ha) of the total area of the three studied landscapes, while 17% (356 ha) was covered by secondary forests of different ages (0.5-25 years). Approximately 50% (1031 ha) of the land surface was allocated to 13 different agricultural land uses (Table A.1). Livestock pastures were the most extensive land use in the three landscapes, representing 85% of the total agricultural land (Table A.1).

Diversity of agricultural land uses varied among landscapes. While in Chajul the agricultural land uses showed the highest values of richness, diversity and evenness, those in Playón de la Gloria exhibited the lowest values (Table 2). The Gini index showed that each landscape, and all landscapes as a group, had a high inequality (*i.e.* Gini values near to one) in the land proportion covered by different land uses. The highest inequality uses were found in Playón de la Gloria, followed by Loma Bonita and Chajul. When we incorporated old-growth forest remnants and secondary forest patches, however, the inequality was reduced a little (Table 2).

3.2. Disturbance regimes produced by agricultural land uses

We found significant differences in field size among land uses ($F_{7,13} = 27.7$, $P \leq 0.001$, Fig. 2a). Livestock pasture had the biggest

Table 2
Diversity of agricultural land uses at three landscapes (villages) and combining them at Marqués de Comillas region, Chiapas, México.

Index	Chajul	Loma Bonita	Playón de la Gloria	All landscapes
Shannon	0.59	0.56	0.48	0.60
Shannon's Evenness	0.62	0.59	0.53	0.54
Simpson	3.21	2.72	2.49	3.18
$Gini_a$*	0.84	0.88	0.89	0.85
$Gini_t$**	0.79	0.82	0.84	0.79

*G_a = considering only agricultural land uses in the landscape; ** G_t = including old-growth forest remnants and secondary forest patches.

size with a mean (±SD) of 15.5 ± 2.9 ha, followed by oil palm plantations (8.7 ha, only present in one of the three studied landscapes), and cocoa plantations (3.3 ± 1.7 ha). Other crops did not exceed 2 ha (Fig. 2a, Table 1). Excluding crops of recent (< 2 years) introduction (*i.e.*, oil palm plantations, vegetable crops, and mahogany plantations), agricultural land-use duration was similar ($F_{7,13}$ = 1.3, $P \geq 0.05$) among land uses (Fig. 2b) with an average of 15.5 ± 5.3 years. Disturbance severity was higher in monocultures (*i.e.*, corn, chili and beans) and livestock pastures than in tree plantations (*i.e.*, cocoa, coffee, fruit orchards; $F_{7,13}$ = 6.8, $P \leq 0.01$, Fig. 2c). Disturbance inflicted by the chili crop was very severe, mainly because of the high use of agrochemicals, the recurrent use of heavy machinery, the burning events and negligible tree cover (Fig. 2c, Table 1). Disturbance severity in pastures was high because of livestock trampling, recurrent use of fire (to promote grass growth) and frequent use of agrochemicals. Pastures, though, had greater tree cover in the field than monocultures (Fig. 2c, Table 1). Disturbance severity was lower in fruit orchards, cocoa and coffee plantations because fires were rare, the tree cover was high, and the land clearing was carried out only by hand weeding or machete.

The recorded agricultural land uses represented a disturbance gradient, ranging from land uses with high EDI values such as pastures and oil palm crop to those with a small EDI value, corresponding to tree plantations: coffee, cocoa and fruit orchards, as in Fig. 2d and Table S1. EDI also varied widely within the same land-use type depending on management characteristics associated with each field (Table 1); see standard deviation values in Fig. 2.

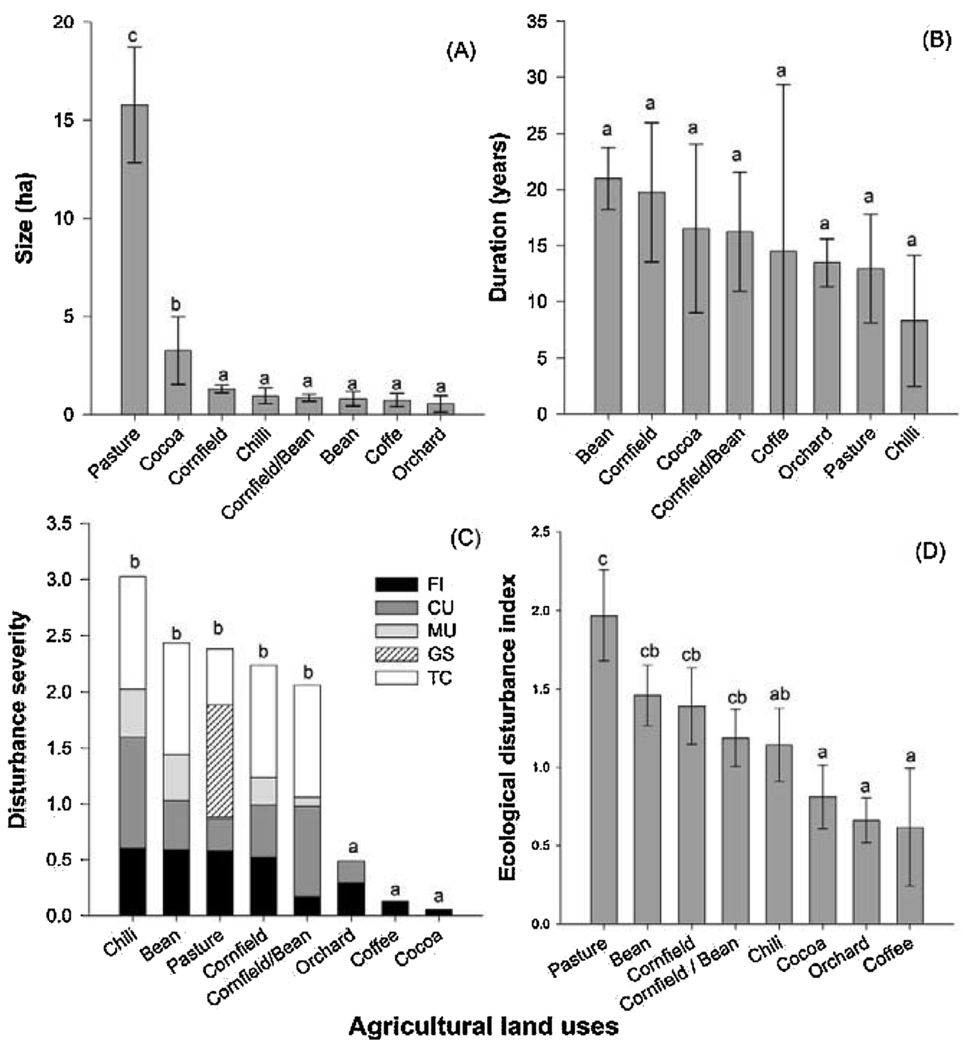

Fig. 2. Ecological disturbance regimes assessed for different agricultural land uses (agricultural land uses) found at the Marqués de Comillas study region, Chiapas. We provide for each agricultural land use the following: (a) field size in hectares, (b) duration under the same land use in years, (c) disturbance severity of land use considering five common management practices and (d) an integrated ecological disturbance index. The bars indicate one standard deviation. Bars not sharing the same letter are significantly different ($P < 0.05$). Components of disturbance severity: FI = Fire incidence, CU = Chemical use, MU = Machinery use, GI = Grazing intensity, TC = Tree cover in the field. Banana, mahogany, oil palm, rice and vegetable land uses are not included in the figures because of their low representativeness in the studied landscapes (n = 1).

3.3. Similarity among agricultural land uses in disturbance regimes

The two main PCA axes explained 89.2% of the total variation among the 156 studied fields. Disturbance severity was highly and positively correlated with axis-1 ($r = 0.99$), while size and duration were positively ($r = 0.86$) and negatively ($r = -0.52$) correlated, respectively, to axis-2. Based on this analysis, three major groups of agricultural land uses with contrasting disturbance regimes were detected (Fig. 3). Coffee, cocoa, mahogany and fruit orchards formed a distinctive group (hereafter called "agroforestry systems") characterized by small size, low to intermediate duration, and low disturbance severity. Annual and biannual monocultures (maize, beans, rice, vegetables, and chili), which are practiced either by crop rotation on the same land or by rotation of the same crop in different land portions, formed a second group. This group was characterized by small size, long duration, and medium to high disturbance severity. Finally, livestock pasture and oil palm (*Elaeis guineensis*) plantations constituted a group (hereafter called "extensive farming") characterized by large size, intermediate to short duration, and high disturbance severity.

3.4. Disturbance regimes and forest regeneration at the landscape level

Loma Bonita was the landscape with the higher ecological disturbance index at the landscape level ($EDI_{wm} = 0.49$) compared to Playón de la Gloria (0.35) and Chajul (0.33). The three landscapes as a group had an intermediate EDI_{wm} value of 0.38. Chajul represented the landscape with the higher land proportion covered with old-growth and secondary forests (Fig. 4).

Biomass, species richness and species diversity, but not stem density of second-growth forest trees, consistently declined as EDI_{wm} increased across our nine 3×3 km landscapes (Fig. 5). Multiple linear regression analysis showed that these relationships were independent of secondary forest age in the landscapes, since all structural forest variables' effect on fallow age was not significant ($P > 0.10$).

4. Discussion

4.1. Diversity of agricultural land uses in modified tropical landscapes

In several Neotropical regions, HMLs have been subjected to a strong process of forest conversion to agriculture (Geist and Lambin, 2002; FAO, 2009; Gibbs et al., 2010). In Marqués de Comillas, in fewer than 45 years almost 70% of the former old-growth forest has been converted to a wide array of agricultural land uses. We found that such conversion was accompanied by the predominant establishment of extensive cattle pastures, which was the land use with the highest ecological disturbance; in abandoned pastures, we recorded the highest reductions in forest regeneration potential at the field level (Zermeño-Hernández et al., 2015). On a larger spatial scale, second-growth forests exhibited the lowest species diversity and biomass in landscapes predominantly covered by pastures (Fig. 5). Pastures are widespread in the Neotropical HMLs, tending to homogenize the landscape (Lambin et al., 2003; Wassenaar et al., 2007). Therefore, the challenge of meeting the demand for agricultural products while conserving biodiversity (Harvey et al., 2008) in HMLs is particularly difficult to achieve under the actual dominance of extensive farming systems. Consequently, the value of HMLs for biodiversity conservation is increasingly under debate (Estrada and Coates-Estrada, 2002; Harvey et al., 2004; Harvey and González-Villalobos, 2007; Melo et al., 2013). Our results, however, support schemes proposing that more diverse and heterogeneous landscapes, with agricultural land uses retaining abundant tree cover of native species (e.g., agroforestry systems), are favorable for forest regeneration and biodiversity conservation (Moguel and Toledo, 1999; Rice and Greenberg, 2000; Finegan and Nasi, 2004; Harvey et al., 2005).

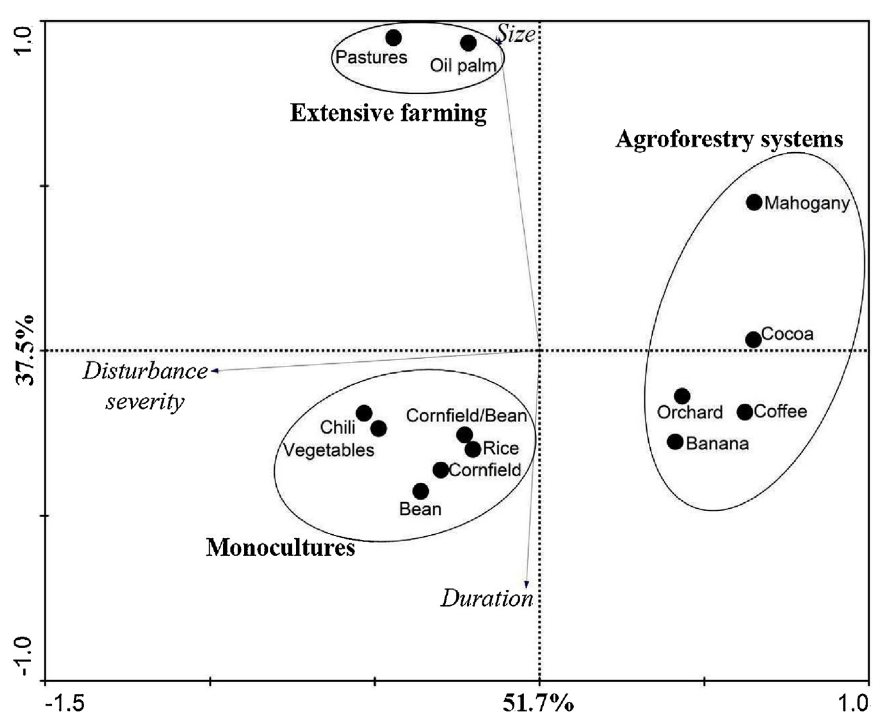

Fig. 3. PCA ordination of agricultural land uses based on components of ecological disturbance regimes in Marqués de Comillas, Chiapas. The values on the axes correspond to the percentage of variance explained by each axis. The length of vectors indicates the percentage of variance explained by each variable, and the arrow direction shows the direction of the relationship (positive or negative) vis-à-vis the axes.

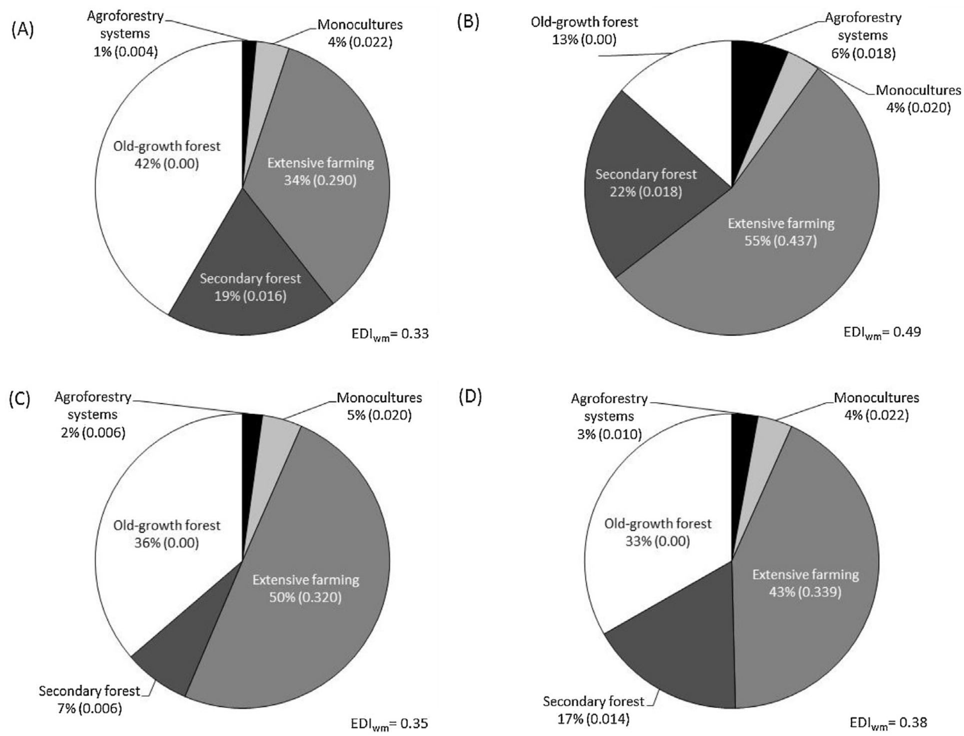

Fig. 4. Composition of land uses in human-modified landscapes (HMLs) in Marqués de Comillas region, southeastern Mexico. The pie graphs denote the percentage of land devoted to three agricultural land-use groups (agroforestry systems, monocultures and extensive farming), secondary patches and old-growth forests in the following HMLs: (A) Chajul, (B) Loma Bonita, (C) Playón de la Gloria landscapes and (D) all landscapes combined. The product of multiplying the EDI value of each agricultural land-use group by the proportion of land covered by that group (p_i) is shown in brackets ($EDI_i{}^*p_i$). At the bottom of each pie graph, the EDI weighted mean (EDI_{wm}), which is the sum of the $EDI_i{}^*p_i$ values in each landscape, is presented.

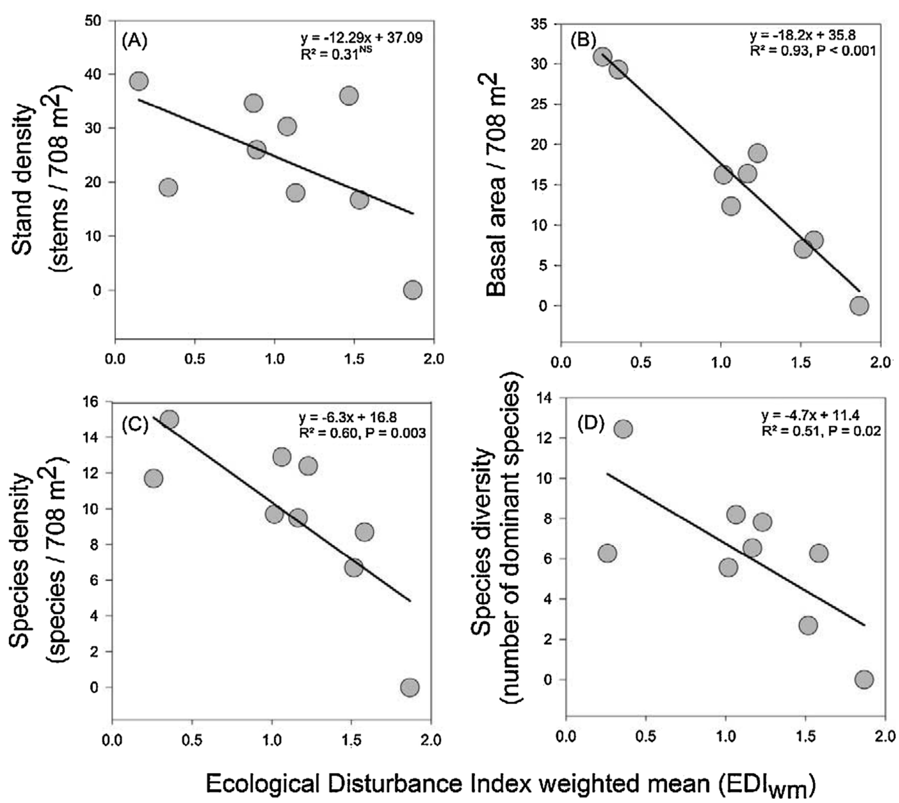

Fig. 5. The change in structural attributes of secondary forests along a gradient of human-modified tropical landscapes differing in ecological disturbance regimes (EDI_{wm}) inflicted by agricultural land uses in Marqués de Comillas, southeastern Mexico. (A) Stem density, (B) basal area, (C) species richness and (D) species diversity (inverse of the Simpson index) of trees (DBH ≥ 10 cm) in nine 3 × 3 km landscapes; in each panel best adjusted regression models, proportion of explained variation (R^2), and statistical significance are provided.

4.2. Disturbance regimes associated with contrasting agricultural land uses

4.2.1. Agroforestry systems

This group of land uses was characterized by low ecological disturbance regimes (i.e. low EDI values). Generally, agroforestry systems are of traditional production, conserve heterogeneous canopies of native tree species (Perfecto et al., 1996; Benton et al., 2003; Perfecto and Vandermeer, 2008), and are maintained by hand weeding. Agroforestry systems produce shaded environments in the understory, reduce temperature and vapor pressure deficit at the ground level (Perfecto et al., 1996; Klein et al., 2002; Harvey et al., 2005; Zermeño-Hernández et al., 2015), and enable high levels of organic matter, nutrient content and diversity of soil organisms (Kennedy and Smith, 1995; Lupwayi et al., 1998; Kladivko, 2001; Jansa et al., 2002; Zermeño-Hernández et al., 2015). In addition, often these systems are located near forest patches with a high diversity of trees species functioning as seed sources (Zermeño-Hernández et al., 2015). All these properties favor the maintenance of abundant and diverse banks of regenerative propagules, including dormant seeds, recently dispersed seeds, seedlings, and resprouts of forest tree species (Estrada et al., 1993, 1994; Estrada et al., 1997; Kennard et al., 2002; Benton et al., 2003), which promote a rapid forest regeneration after agriculture abandonment. In Marqués de Comillas, Zermeño-Hernández *at al.* (2015) documented that tree density and species diversity of regenerating forests increased more rapidly in recently abandoned agroforestry fields than in cornfields and pastures. In line with this, in Costa Rica, biomass and species diversity of secondary forests of 25–30 years grown in abandoned coffee plantations were similar to those of old-growth forest, even when these plantations had been used for decades (Pascarella et al., 2000).

4.2.2. Monoculture systems

This group included agricultural land uses with intermediate levels of ecological disturbance. The relatively high EDI values for monocultures were mostly because of high disturbance severity. Agrochemicals and machinery used in monocultures negatively affect the structure of vegetation (Andreasen et al., 1996), as well as the diversity of vertebrates (Relyea, 2005) and invertebrates (Haughton et al., 1999; Wardle et al., 1999; Klein et al., 2002). Although the small size (<2 ha) of monocultures and their closeness to riparian vegetation may favor the arrival of seeds dispersed by animals into the fields (Saunders and de Rebeira, 1991; Quintana-Ascencio et al., 1996; Thomlinson et al., 1996), the application of agrochemicals and fire may limit the migration of many animals (including seed dispersers) to monocultures (Perfecto and Vandermeer, 2008). Frequent burning produces soil acidity, the loss of carbon and nitrogen from the soil (Celedón-Muñiz, 2006; Zermeño-Hernández et al., 2015), and the depletion of propagules of native forest species (Kennard et al., 2002). Such detrimental effects are exacerbated by the typical long duration of monocultures (Ewel, 1980; Allen, 1985; Eden et al., 1991; Martins et al., 1991), as was the case in our study region. Using EDI and an experimental system, Zermeño-Hernández et al. (2015) proved that forest regeneration potential in abandoned monocultures is lower than in abandoned agroforestry fields.

4.2.3. Extensive farming

This group included land uses with harsher ecological disturbance regimes. The high EDI values for pastures and oil palm plantations were mostly caused by their large size and high disturbance severity. In extensive pastures, seed dispersal of native tree species, especially of large-seeded ones, is confined to areas close to remnant forest vegetation (Holl, 1999; Cubiña and Aide, 2001). As a result, seed rain in pastures is often low in abundance and diversity (Holl and Lulow, 1997; Holl, 1999; Martínez-Garza and González-Montagut, 1999; Cubiña and Aide, 2001), which is a major barrier for forest regeneration (Holl, 2007). Although isolated trees in pastures may act as attractors of animals that disperse seeds (Guevara et al., 2004; Murray et al., 2008), playing the role of potential regeneration nuclei (Zahawi and Augspurger, 1999; Guevara et al., 2004; Murray et al., 2008; García-Orth and Martínez-Ramos, 2011), several factors can limit this function. For example, seed predation by insects and vertebrates is intense in pastures (Corzo Domínguez, 2007; Garcia-Orth and Martinez-Ramos, 2008), frequent fires eliminate soil seeds (López-Toledo and Martínez-Ramos, 2011), and cattle grazing and trampling eliminate emerging seedlings and young trees. Furthermore, cattle affect soil structure and quality (Buschbacher et al., 1988; Holl, 1999; Martínez and Zinck, 2004), limiting germination or establishment of rain forest plants (Trouse and Humbert, 1961; Sun and Dickson, 1996). After abandonment, regenerating plants are exposed to water and heat stress, which affect their growth and survival (Garcia-Orth and Martinez-Ramos, 2008). All these conditions result in very low regeneration rates in abandoned pastures (Zermeño-Hernández et al., 2015). In Marqués de Comillas, six years after abandonment, abundance, biomass and species richness of tree communities were two to nine times lower in pastures than in cornfields (Martínez-Ramos et al., 2016, in press). In Brazil, secondary forests in abandoned pastures were monopolized by *Vismia* species, and after 25 years species diversity and biomass were much lower than in abandoned clear-cut stands (Mesquita et al., 2015). Furthermore, in acidic and low fertility soils, cattle pastures subjected to recurrent fires are infested by weed species which propagate profusely, which arrests forest regeneration (see also Robiglio and Sinclair, 2011; Suazo-Ortuño et al., 2015).

Disturbance caused by extensive oil palm plantations (frequent use of fire, high amounts of fertilizers and pesticides, and lack of tree cover) are expected to cause similar negative effects on forest regeneration than disturbance caused by pastures. For example, in Costa Rica, secondary forests grown on abandoned palm plantations (*Bactris gasipaes*) had lower abundance and biomass of rain forest trees than secondary forests of the same age regenerating in abandoned cocoa plantations (Fernandes and Sanford, 1995). Therefore, overall, we conclude that extensive farming may impose the strongest barriers to natural forest regeneration after agriculture abandonment (Fernandes and Sanford, 1995; Fujisaka et al., 1998; Zermeño-Hernández et al., 2015).

4.3. Disturbance regimes and forest regeneration at the landscape level

According to our ecological disturbance weighted mean index (EDI_{wm}), the three studied landscapes differed importantly in their agricultural land-use diversity and, hence, in the potential to affect forest regeneration. The prediction that landscapes with higher EDI_{wm} have lower forest regeneration potential was supported by our results when applied to our nine 3×3 km landscapes. The observed reduction in biomass and species diversity of secondary forests as EDI_{wm} increased (Fig. 5) may be caused by changes in the magnitude of two major determinants of forest regeneration: propagule availability (seed sources present in old-growth forest remnants) and the harshness of the environmental conditions at the time of field abandonment. As old-growth forests are reduced in the landscape, fewer species are available for regeneration, which may reduce the effective number of species colonizing second-growth forests (Dalle and de Blois, 2006). Similarly, Zermeño-Hernández et al. (2015) showed that forest regeneration potential was low in abandoned fields where land use inflicted extensive and severe disturbances, such as cattle pastures which had the highest EDI values among the land uses we assessed in Marqués de Comillas (Fig. 2d); the harsh environmental conditions prevailing in abandoned pastures limits the establishment and growth of several native rain forest species (Martínez-Ramos et al., in press). The EDI_{wm} values were largely determined by the percentage of land covered by pastures since this land use encompassed between 7 and 93% of the area of studied landscapes. Considering these facts, it is possible that the secondary forests of low diversity and biomass we found in the landscapes with high EDI_{wm} were developed in abandoned pastures with a scarce forest matrix. Further studies, however, are needed to test this idea.

EDI_{wm} is an attempt to assess in an integrative way the impact of the diversity of agricultural land uses on forest regeneration at the landscape scale, but there are caveats that need to be addressed. First, EDI is based on information provided by landowners and farmers; a double-checking procedure would be necessary to calibrate such information. For example, field size can be corroborated with ground-based measurements and land-use duration with historical aerial photographs or remote sensing techniques (comparing a temporal series of satellite images), where available. Second, because EDI was constructed considering only the last agricultural land use, this index omits other uses endured by the field during its agricultural history, which could contribute to shaping the agricultural legacies on forest regeneration. For example, differences in the temporal sequence of different agricultural land uses can result in different regenerative pathways (Suazo-Ortuño et al., 2015). Another issue for future work is the assignation of EDI_{wm} values to secondary forests, which in this study were assumed to be constant. It is known, however, that species diversity of plants (Chazdon et al., 2007) and animals (de la Pena-Cuéllar et al., 2012; Hernández-Ordóñez et al., 2015), as well as the supply of ecosystem services (such as carbon gain and storage) of secondary forests, increases with fallow age (Poorter et al., 2016). Therefore, the EDI value of secondary forests could decrease with fallow age from a starting value, defined by the land-use history before field abandonment (Mesquita et al., 2015; Zermeño-Hernández et al., 2015), to 0 when secondary forests reach similar ecological attributes of the old-growth forest. Nevertheless, these caveats, Zermeño-Hernández et al. (2015) have shown that this simple, accessible, and inexpensive EDI index predicted forest regeneration potential as well as precise measurements of microclimate and soil conditions taken at the time of field abandonment, which are costly (*e.g.*, equipment requirement) and time-consuming. EDI is especially useful when rapid assessment of ecological disturbance regimes, found in many agricultural fields in HMLs, is required.

5. Concluding remarks

In the hope of finding tropical HMLs where conserving biodiversity and agricultural production coincide, our results highlight the importance of identifying groups of agricultural land uses and landscape composition (proportions of land covered by agricultural land uses, secondary forest and old-growth forest) that may contribute to this goal. Our EDI and ED_{wm} are helpful in this regard. We found that agricultural land uses with low EDI values allow the best forest regeneration. Traditional agroforestry systems are as promissory as those agricultural land-uses favoring forest regeneration. The positive relationship between species diversity and biomass of second-growth forest with the proportion of old-growth forest remaining in the landscape suggests that the maintenance of old-growth forest remnants in the landscape is important for regeneration potential and ecological quality of secondary forests, although more studies are needed to support this idea. Thus, a promising conformation of HMLs would be a mosaic of agricultural land uses with low EDI embedded in a matrix of old-growth and second-growth forests. It is an extraordinary challenge, however, to change the present pathway of the increasing dominance of extensive farming into such a mosaic. This change will depend on solving a complex and conflicting set of societal, economic and ecological factors (Castillo and Toledo, 2000; Perfecto and Vandermeer, 2008). EDI_{wm} can be useful as a tool to identify landscape conformations and land management strategies (e.g. land sharing vs. land sparing; Phalan et al., 2011) which favor biodiversity conservation. Including societal and economical dimensions, though, is required for finding positive balances between agricultural production and biodiversity conservation. In this context, farmers, policy makers and landscape managers should focus not only on promoting agricultural land uses with low EDI, but also in restoring degraded lands and promoting the sustainable use of the goods and services provided by second-growth forests (Schroth and Harvey, 2007; Chazdon, 2014).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.06.007.

References

Aide, T.M., Clark, M.L., Grau, H.R., López-Carr, D., Levy, M.A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M.J., Muñiz, M., 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45, 262–271.

Allen, J., 1985. Soil response to forest clearing in the United States and the tropics: geological and biological factors. Biotropica 17, 15–27.

Andreasen, C., Stryhn, H., Streibig, J.C., 1996. Decline of the flora in Danish arable fields. J. Appl. Ecol. 33, 619–626.

Barbier, E.B., Burgess, J.C., 1996. Economic analysis of deforestation in Mexico. Environment and Development Economics 1, 203–239.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182–188.

Buschbacher, R., Uhl, C., Serrao, E.A.S., 1988. Abandoned pastures in eastern Amazonia: II. Nutrient stocks in the soil and vegetation. J. Ecol. 76, 682–699.

Castillo, A., Toledo, V.M., 2000. Applying ecology in the third world: the case of Mexico. Bioscience 50, 66–76.

Castillo-Santiago, M.A., Ricker, M., de Jong, B.H., 2010. Estimation of tropical forest structure from SPOT-5 satellite images. Int. J. Remote Sens. 31, 2767–2782.

Celedón-Muñiz, H., 2006. Impacto del sistema agrícola de roza, tumba y quema sobre las características de tres unidades de suelo en la Selva Lacandona de Chiapas. Facultad de Ciencias. Universidad Nacional Autónoma de México, México, pp. 122.

Challenger, A., Soberón, J., 2008. Los ecosistemas terrestres. Capital natural de México 1, 87–108.

Chazdon, R.L., Letcher, S.G., van Breugel, M., Martínez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of changes in tree communities of secondary Neotropical forests following major disturbances. Philosophical Transactions of the Royal Society B 362, 273–289.

Chazdon, R.L., 2014. Second Growth: The Promise of Tropical Forest Regeneration in an Age of Deforestation. University of Chicago Press.

Colwell, R.K., 2009. EstimateS v. 8.2.0: Statistical estimation of species richness and shared species from samples. User's Guide and Application, . htpp://viceroy. eeb. uconn. edu/estimates.
Corzo Domínguez, A., 2007. Papel de la depredación de semillas en el establecimiento de plántulas en bosques secundarios tropicales. Posgrado en Ciencias Biológicas. Universidad Nacional Autónoma de México, México, D.F.
Cramer, V.A., Hobbs, R.J., Standish, R.J., 2008. What's new about old fields?: Land abandonment and ecosystem assembly. Trends in Ecology & Evolution 23, 104–112.
Crawley, M.J., 1993. GLIM for Ecologists Methods in Ecology. Blackwell Scientific Publications.
Cubiña, A., Aide, T.M., 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. Biotropica 33, 260–267.
Dalle, S.P., de Blois, S., 2006. Shorter fallow cycles affect the availability of noncrop plant resources in a shifting cultivation system. Ecol. Soc. 11, 2.
De Jong, B.H., Ochoa-Gaona, S., Castillo-Santiago, M.A., Ramírez-Marcial, N., Cairns, M.A., 2000. Carbon flux and patterns of land-use/land-cover change in the Selva Lacandona: mexico. AMBIO 29, 504–511.
De Vos, J., 1980. La paz de Dios y del rey: la conquista de la selva lacandona, 1525–1821. Gobierno del estado de Chiapas .
DeFries, R., Hansen, A., Turner, B., Reid, R., Liu, J., 2007. Land use change around protected areas: management to balance human needs and ecological function. Ecol. Appl. 17, 1031–1038.
Eden, M., Furley, P., McGregor, D., Milliken, W., Ratter, J., 1991. Effect of forest clearance and burning on soil properties in northern Roraima, Brazil. Forest Ecology and Managemen .
Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biol. Conserv. 103, 237–245.
Estrada, A., Coates-Estrada, R., Meritt, D., 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16, 309–318.
Estrada, A., Coates-Estrada, R., Meritt, D., 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. Ecography 17, 229–241.
Estrada, A., Coates-Estrada, R., Meritt, D.A., 1997. Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodiversity and Conservation 6, 19–43.
Ewel, J., 1980. Tropical succession: manifold routes to maturity. Biotropica 12, 2–7.
FAO, 2009. Situación De Los Bosques Del Mundo, 2009. Food & Agriculture Org., Roma, Italia.
Fernandes, D.N., Sanford, R.L., 1995. Effects of recent land-use practices on soil nutrients and succession under tropical wet forest in Costa Rica. Conserv. Biol. 9, 915–922.
Finegan, B., Nasi, R., 2004. The biodiversity and conservation potential of shifting cultivation landscapes. In: Schroth, G., da Fonseca, G.A.B., Harvey, C., Gascon, C., Vasconcellos, H.L., Izac, M.-A.N. (Eds.), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, pp. 153–197.
Fujisaka, S.A.M., Escobar, G., Veneklaas, E., 1998. Plant community diversity relative to human land uses in an Amazon forest colony. Biodiversity and Conservation 7, 41–57.
García-Orth, X., Martínez-Ramos, M., 2011. Isolated trees and grass removal improve performance of transplanted *Trema micrantha* (L.) Blume (Ulmaceae) saplings in tropical pastures. Restor. Ecol. 19, 24–34.
Garcia-Orth, X., Martinez-Ramos, M., 2008. Seed dynamics of early and late successional tree species in tropical abandoned pastures: seed burial as a way of evading predation. Restor. Ecol. 16, 435–443.
Gastwirth, J.L., 1972. The estimation of the Lorenz curve and Gini index. Rev. Econ. Stat. 306–316.
Geist, H.J., Lambin, E.F., 2002. Proximate Causes and Underlying Driving Forces of Tropical Deforestation Tropical forests are disappearing as the result of many pressures, both local and regional, acting in various combinations in different geographical locations. Bioscience 52, 143–150.
Gibbs, H.K., Ruesch, A., Achard, F., Clayton, M., Holmgren, P., Ramankutty, N., Foley, J., 2010. Tropical forests were the primary sources of new agricultural land in the 1980 and 1990. Proc. Natl. Acad. Sci. 107, 16732–16737.
Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J., Laurance, W.F., Lovejoy, T.E., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.
Guevara, S., Laborde, J., Sánchez-Rios, G., 2004. Rain forest regeneration beneath the canopy of fig trees isolated in pastures of Los Tuxtlas, Mexico. Biotropica 36, 99–108.
Harvey, C.A., González-Villalobos, J.A., 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodiversity and Conservation 16, 2257–2292.
Harvey, C.A., Tucker, N.I.J., Estrada, A., 2004. Live Fences, Isolated Trees, and Windbreaks: Tools for Conserving Biodiversity in Fragmented Tropical Landscapes. Island Press, Washington, DC.
Harvey, C.A., Villanueva, C., Villacís, J., Chacón, M., Muñoz, D., López, M., Ibrahim, M., Gómez, R., Taylor, R., Martinez, J., 2005. Contribution of live fences to the ecological integrity of agricultural landscapes. Agriculture Ecosystems Environment 111, 200–230.
Harvey, C., Komar, O., Chazdon, R., Ferguson, B., Finegan, B., Griffith, D., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., 2008. Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conserv. Biol. 22, 8–15.
Haughton, A.J., Bell, J.R., Boatman, N.D., Wilcox, A., 1999. The effects of different rates of the herbicide glyphosate on spiders in arable field margins. The Journal of Arachnology 27, 249–254.
Hernández-Ordóñez, O., Urbina-Cardona, N., Martínez-Ramos, M., 2015. Recovery of amphibian and reptile assemblages during OldáField succession of tropical rain forests. Biotropica 47, 377–388.
Holl, K., Lulow, M., 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. Biotropica 29, 459–468.
Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.
Holl, K.D., 2007. Old field vegetation succession in the neotropics. In: Cramer, V., Hobbs, R. (Eds.), Old Fields. Dynamics and Restoration of Abandoned Farmland. Island Press, Washington, D.C., USA, pp. 93–118.
Houghton, R.A., 1994. The worldwide extent of land-use change. Bioscience 44, 305–313.
Jansa, J., Mozafar, A., Anken, T., Ruh, R., Sanders, I., Frossard, E., 2002. Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12, 225–234.
Kennard, D.K., Gould, K., Putz, F.E., Fredericksen, T.S., Morales, F., 2002. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. For. Ecol. Manage. 162, 197–208.
Kennedy, A.C., Smith, K.L., 1995. Soil microbial diversity and the sustainability of agricultural soils. Plant and Soil 170, 75–86.
Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil & Tillage Research 61, 61–76.
Klein, A.M., Steffan-Dewenter, I., Buchori, D., Tscharntke, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. Conserv. Biol. 16, 1003–1014.
López-Toledo, L., Martínez-Ramos, M., 2011. The soil seed bank in abandoned tropical pastures: source of regeneration or invasion? Revista Mexicana de Biodiversidad 82, 663–678.
Lambin, E.F., Geist, H.J., Lepers, E., 2003. Dynamics of land-use and land-cover change in tropical regions. Annu. Rev. Environ. Resour. 28, 205–241.
Lepers, E., Lambin, E.F., Janetos, A.C., DeFries, R., Achard, F., Ramankutty, N., Scholes, R.J., 2005. A synthesis of information on rapid land-cover change for the period 1981–2000. Bioscience 55, 115–124.
Lupwayi, N.Z., Rice, W.A., Clayton, G.W., 1998. Soil microbial diversity and community structure under wheat as influenced by tillage and crop rotation. Soil Biol. Biochem. 30, 1733–1741.
Magurran, A.E., 2004. Measuring Biological Diversity. Whiley-Blackwell.
Martínez, L.J., Zinck, J.A., 2004. Temporal variation of soil compaction and deterioration of soil quality in pasture areas of Colombian Amazonia. Soil & Tillage Research 75, 3–18.
Martínez-Garza, C., González-Montagut, R., 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecology 145, 255–265.
Martínez-Ramos, M., Anten, N.P., Ackerly, D.D., 2009. Defoliation and ENSO effects on vital rates of an understorey tropical rain forest palm. J. Ecol. 97, 1050–1061.
Martínez-Ramos, M., Pingarroni, A., Rodríguez-Velázquez, J., Toledo-Chelala, L., Zermeño-Hernández, I., Bongers, F. Natural forest regeneration and ecological restoration in human modified tropical landscapes. Biotropica (in press).
Martins, P., Cerri, C., Volkoff, B., Andreux, F., Chauvel, A., 1991. Consequences of clearing and tillage on the soil of a natural Amazonian ecosystem. For. Ecol. Manage. 38, 202–273.
Melo, F.P., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., Tabarelli, M., 2013. On the hope for biodiversity-friendly tropical landscapes. Trends in Ecology & Evolution 28, 462–468.
Mendoza, E., Dirzo, R., 1999. Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. Biodiversity & Conservation 8, 1621–1641.
Mesquita, R.d.C.G., dos Santos Massoca, P.E., Jakovac, C.C., Bentos, T.V., Williamson, G.B., 2015. Amazon rain forest succession: stochasticity or land-Use legacy? Bioscience 65, 849–861.
Moguel, P., Toledo, V.M., 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conserv. Biol. 13, 11–21.
Murray, K., Winnett-Murray, K., Roberts, J., Horjus, K., Haber, W., Zuchowski, W., Kuhlmann, M., Long-Robinson, T., 2008. The roles of disperser behavior and physical habitat structure in regeneration of post-Agricultural fields. In: Myster, R.W. (Ed.), Post-agricultural Succession in the Neotropics. Springer, Puerto Rico, pp. 192–215.
Norden, N., Angarita, H.A., Bongers, F., Martínez-Ramos, M., Granzow-de la Cerda, I., van Breugel, M., Lebrija-Trejos, E., Meave, J.A., Vandermeer, J., Williamson, G.B., 2015. Successional dynamics in Neotropical forests are as uncertain as they are predictable. Proc. Natl. Acad. Sci. 112.
Pascarella, J.B., Aide, T.M., Serrano, M.I., Zimmerman, J.K., 2000. Land-use history and forest regeneration in the Cayey mountains, Puerto Rico. Ecosystems 3, 217–228.
Perfecto, I., Vandermeer, J., 2008. Biodiversity conservation in tropical agroecosystems: a new conservation paradigm. Annual New York Academy Science 1134, 173–200.
Perfecto, I., Rice, R.A., Greenberg, R., Van der Voort, M.E., 1996. Shade coffee: a disappearing refuge for biodiversity. Bioscience 46, 598–599.
Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333, 1289–1291.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics: An Introduction. Academic Press, San Diego, California, USA.

Poorter, L., Bongers, F., Aide, T.M., Zambrano, A.M.A., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H., Broadbent, E.N., Chazdon, R.L., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214.

Quezada, M.L., Arroyo-Rodríguez, V., Pérez-Silva, E., Aide, T.M., 2014. Land cover changes in the Lachuá region, Guatemala: patterns, proximate causes, and underlying driving forces over the last 50 years. Reg. Environ. Change 1–11.

Quintana-Ascencio, P.F., Gonzalez-Espinosa, M., Ramirez-Marcial, N., Dominguez-Vazquez, G., Martinez-Ico, M., 1996. Soil seed banks and regeneration of tropical rain forest from milpa fields at the Selva Lacandona Chiapas, Mexico. Biotropica 28, 192–209.

R-Core-Team-R, 2015. In: Computing, Computing, R.F.f.S. (Eds.), R: A Language and Environment for Statistical Computing. Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Relyea, R.A., 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. Ecol. Appl. 15, 618–627.

Rice, R.A., Greenberg, R., 2000. Cacao cultivation and the conservation of biological diversity. AMBIO 29, 167–173.

Robiglio, V., Sinclair, F., 2011. Maintaining the conservation value of shifting cultivation landscapes requires spatially explicit interventions. Environ. Manage. 48, 289–306.

Saunders, D.A., de Rebeira, C.P., 1991. Values of corridors to avian populations in a fragmented landscape. Nature Conservation 2, 221–240.

Schroth, G., Harvey, C.A., 2007. Biodiversity conservation in cocoa production landscapes: an overview. Biodiversity and Conservation 16, 2237–2244.

Siebe, C., Martínez-Ramos, M., Segura-Warnholtz, G., Rodríguez-Velázquez, J., Sánchez-Beltrán, S., 1996. Soil and vegetation patterns in the tropical rainforest at Chajul Southeast Mexico. Proceedings of the International Congress on Soil of Tropical Forest Ecosystems 3rd Conference on Forest Soils (ISSS-AISS-IBG), Mulawarman University Press, Indonesia, pp. 40–58.

Suazo-Ortuño, I., Lopez-Toledo, L., Alvarado-Díaz, J., Martínez-Ramos, M., 2015. Landñuse change dynamics, soil type and species forming monoñdominant patches: the case of pteridium aquilinum in a neotropical rain forest region. Biotropica 47, 18–26.

Sun, D., Dickson, G.R., 1996. The competition effect of *Brachiaria decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in tropical North Australia. Biotropica 28, 272–276.

Thomlinson, J.R., Serrano, M.I., Lopez, T.M., Aide, T.M., Zimmerman, J.K., 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). Biotropica 28, 525–536.

Trouse, A.C., Humbert, R.P., 1961. Some effects of soil compaction on the development of sugar cane roots. Soil Sci. 91, 208–217.

Walker, R., Moran, E., Anselin, L., 2000. Deforestation and cattle ranching in the Brazilian Amazon: external capital and household processes. World Development 28, 683–699.

Wardle, D.A., Nicholson, K.S., Bonner, K.I., Yeates, G.W., 1999. Effects of agricultural intensification on soil-associated arthropod population dynamics, community structure, diversity and temporal variability over a seven-year period. Soil Biol. Biochem. 31, 1691–1706.

Wassenaar, T., Gerber, P., Verburg, P., Rosales, M., Ibrahim, M., Steinfeld, H., 2007. Projecting land use changes in the Neotropics: the geography of pasture expansion into forest. Global Environ. Change 17, 86–104.

Willhauck, G., Schneider, T., De Kok, R., Ammer, U., 2000. Comparison of object oriented classification techniques and standard image analysis for the use of change detection between SPOT multispectral satellite images and aerial photos. Proceedings of XIX ISPRS Congress, Citeseer, pp. 35–42.

Zahawi, R.A., Augspurger, C.K., 1999. Early plant succession in abandoned pastures in Ecuador. Biotropica 31, 540–552.

de la Pena-Cuéllar, E., Stoner, K.E., Avila-Cabadilla, L.D., Martínez-Ramos, M., Estrada, A., 2012. Phyllostomid bat assemblages in different successional stages of tropical rain forest in Chiapas, Mexico. Biodiversity and Conservation 21, 1381–1397.

van Breugel, M., Martínez-Ramos, M., Bongers, F., 2006. Community dynamics during early secondary succession in mexican tropical rain forest. J. Trop. Ecol. 22, 663–674.

Zermeño-Hernández, I., Méndez-Toribio, M., Siebe, C., Benítez-Malvido, J., Martínez-Ramos, M., 2015. Ecological disturbance regimes caused by agricultural land uses and their effects on tropical forest regeneration. Appl. Veg. Sci. 18, 443–455.