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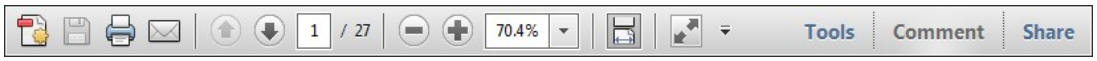

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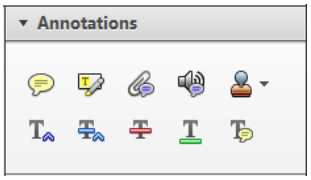

1. Replace (Ins) Tool – for replacing text.

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- Highlight a word or sentence.
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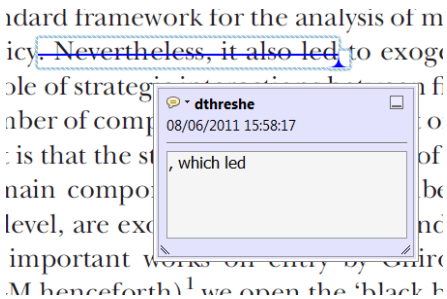

2. Strikethrough (Del) Tool – for deleting text.

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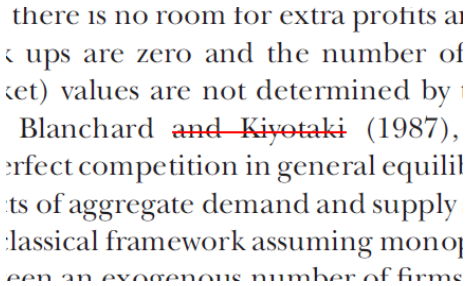

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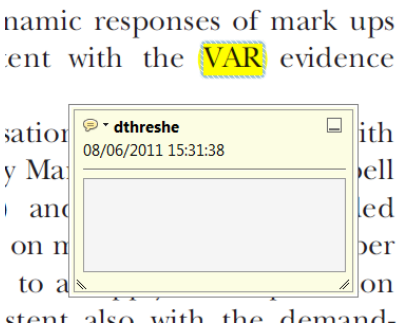

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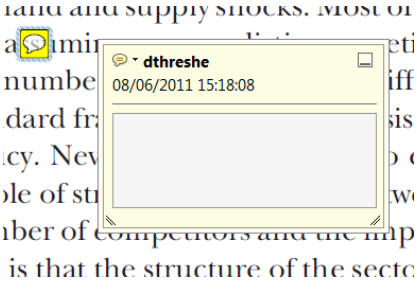

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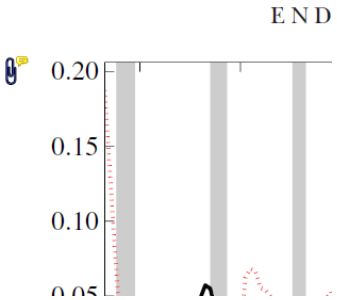

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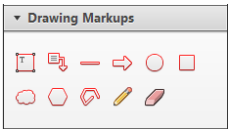

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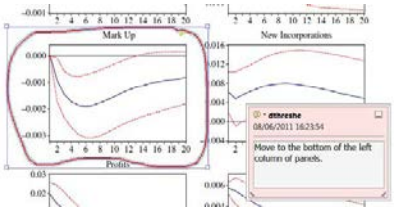

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REVIEW

Natural forest regeneration and ecological restoration in human-modified tropical landscapes

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ABSTRACT

In human-modified tropical landscapes (HMLs) the conservation of biodiversity, functions and services of forest ecosystems depends on persistence of old growth forest remnants, forest regeneration in abandoned agricultural fields, and restoration of degraded lands. Understanding the impacts of agricultural land uses (ALUs) on forest regeneration is critical for biodiversity conservation in HMLs. Here, we develop a conceptual framework that considers the availability of propagules and the environment prevailing after field abandonment as two major determinants of forest regeneration in HMLs. The framework proposes that regeneration potential decreases with size, duration and severity of agricultural disturbance, reducing propagule availability and creating ill-suited environmental conditions for regeneration. We used studies from Southern Mexico to assess this framework. First, we identify regeneration bottlenecks that trees face during transit from seed to follow-up life stages, using demographic analysis of dominant pioneer species in recently abandoned fields. Then, we explore effects of ALUs on forest regeneration at the field and landscape scales, addressing major legacies. Finally, we integrate agricultural disturbance with landscape composition to predict attributes of successful second growth forests in HMLs, and provide indicators useful to select tree native species for active restoration. An indicator of disturbance inflicted by ALUs, based on farmers' information, predicted better regeneration potential than measurements of soil and microclimate conditions at time of abandonment. Cover of cattle pastures in the landscape was a stronger indicator of forest regenerating attributes than cover of old growth forest remnants. To conclude, we offer recommendations to promote forest regeneration and biodiversity conservation in HMLs.

Abstract in Spanish is available with online material.

Key words: agricultural land uses; dispersal limitation; establishment limitation; Mexico; secondary succession; second growth forests; tree demography; tropical rain forest.

TROPICAL LANDSCAPES ARE INCREASINGLY COMPOSED OF OLD GROWTH FOREST REMNANTS immersed in a matrix of agricultural land uses, patches of second growth forests, and degraded lands (Laurance *et al.* 2014). In such human-modified landscapes (HMLs) the conservation of biodiversity, functions, and services of forest ecosystems critically depends on the persistence of old growth forest fragments (Laurance & Peres 2006), the potential for forest regeneration in abandoned fields (Chazdon 2014, Chazdon & Uriarte 2016), and the restoration of degraded lands (Holl 2012). Fragments often are <100-ha and undergo ecosystem degradation due to edge effects and other threats (Benitez-Malvido & Martínez-Ramos 2003, Laurance *et al.* 2006, 2007). Ways to prevent further degradation of forest fragments, often-important biodiversity pools (Turner & Corlett 1996, Arroyo-Rodríguez *et al.* 2013), are urgently needed (Laurance *et al.* 2002). Forest regeneration potential can be limited by disturbance effects caused by extensive, severe, and long-lasting agricultural land uses (Holl 2007, Zermeño-Hernández *et al.* 2015, Zermeño-Hernández & Martínez-Ramos 2016). Therefore, understanding ecological legacies of agricultural land uses (Chazdon 2003, Foster *et al.* 2003), identifying land uses that promote forest regeneration, and developing ecological tools to restore degraded lands (Hobbs & Harris 2001, Hobbs & Cramer 2007, Holl 2012, Gilman *et al.* 2016) are critical for constructing positive scenarios of agricultural production, biodiversity conservation, and enhancement of rural livelihoods in HMLs (Finegan & Nasi 2004, DeFries *et al.* 2007, Melo *et al.* 2013, Adams *et al.* 2016, Lazos *et al.* 2016,).

In this paper, we focus on three interlinked themes on natural forest regeneration and restoration in HMLs: (1) regeneration bottlenecks for colonizing tree species; (2) effects of land use legacies on forest regeneration; and (3) maximizing the success of natural regeneration and restoration. The first topic approaches natural regeneration of pioneer species in recently abandoned agricultural fields; the idea is to pinpoint ecological factors that play critical roles for dispersal and establishment of colonizing

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pioneer tree species, which are dominant in young second growth forests. In the second theme, we assess legacies of disturbance regimes inflicted by different agricultural land uses on forest regeneration with the idea of identifying those uses enabling best regeneration at the local (field) scale. Third, we integrate the landscape composition with the disturbance regimes associated with different agricultural land uses to predict structural attributes (density, biomass, species diversity) of second growth forests in HMLs; also, we provide guidelines for identifying native tree species that can help in restoration of degraded lands. We approach these issues mostly using studies conducted in an important wet lowland tropical forest area in Mexico. To start, we describe a general conceptual framework reflecting our main contribution. Then, we present results on the three selected themes. As concluding remarks, we give recommendations for promoting forest regeneration and conserving biodiversity in HMLs.

CONCEPTUAL FRAMEWORK

Tropical rain forest species evolved under the influence of chronic small-scale natural disturbances (Martínez-Ramos 1985, Denslow 1987). Tree and limb falls create gaps in the forest canopy and play a critical role in the forest regeneration cycle, through which the structure and composition of plant populations and communities change in space and time (Whitmore 1984, Martínez-Ramos *et al.* 1988). Deforestation and subsequent agricultural land uses, in contrast, generate disturbances of much larger size, severity, and duration (Foster *et al.* 2003, Holl & Aide 2011, Laurance *et al.* 2014). Such anthropogenic disturbances are new events in the evolutionary history of rain forest tree species for which most of them have poor or null adaptive responses and thus might limit their natural regeneration. Commonly, agricultural land uses eliminate the original forest ecosystem and reduce the potential for forest regeneration in the abandoned fields (Hooper *et al.*, 2002, Holl 2012). Figure 1 illustrates how the increase in disturbance inflicted by agricultural land use (from left to right) affects two major forest regeneration determinants: the availability of propagules (soil seeds, seed rain, seedling, sapling and re-sprouting banks) and the biophysical conditions prevailing at the time of field abandonment (Holl 2007, Martínez-Ramos & García-Orth 2007). With increasing agricultural disturbance, bottlenecks acting on regenerating species are expected to become stricter. For example, propagule availability is expected to decline due to dispersal limitation as the size of the agricultural field and distance to forest remnants (*i.e.*, seed sources) increase. Also, dispersal limitation is exacerbated with less forest remaining in the periphery of the field. Such effects are expected to be most limiting for large seeded species that depend on animals for seed dispersal (see decreasing size of bird image in Fig. 1, indicating lower dispersal potential with increasing agricultural disturbance). Other studies have shown that animal-dispersed species decrease their representation in the seed rain with increasing distance to forest-remnant edges (Aide & Cavelier 1994, Holl 1999). Also, establishment limitation enhances with the disturbance duration and severity (particularly frequent use of fire) of agricultural uses (*e.g.,* cattle pastures and conventional monocultures in Fig. 1), which also deplete *in situ* propagule pools (*e.g.,* Quintana-Ascencio *et al.* 1996, Holl 2007, Martínez-Ramos & García-Orth 2007, see reduction in gray boxes in the sketch). At the same time, biophysical environmental conditions depart from those enabling the survival, growth and or reproduction of most rain forest plants (Chazdon 2003, Zermeño-Hernández *et al.* 2015); thus, few tolerant pioneer species become dominant in abandoned fields with harsh environmental conditions (*e.g.,* Mesquita *et al.* 2015). Under extreme disturbance condition, severe field degradation occurs, including the possible field infestation by weeds impeding forest regeneration (Fig. 1; *e.g.,* Suazo-Ortuño *et al.* 2015). In such circumstance, time to regeneration is uncertain and active ecological restoration is required to achieve desirable ecosystem properties. With increasing harshness of agricultural land use the values of biodiversity, functions and services of regenerating forest reduces and the costs associated to restoration increase (Fig. 1; Chazdon 2008).

In the following sections, we develop the framework by analyzing the demography of typical pioneer tree species and illustrating the nature of bottlenecks affecting forest regeneration in recently abandoned agricultural fields, where disturbance conditions were not severe. Then, we assess how increasing levels of agricultural disturbance affect forest regeneration potential, identifying key local and landscape factors affecting the structure and composition of regenerating second growth forests. A special effort is directed to provide simple, low-cost, and effective, useful indicators that help to identify agricultural land uses and HMLs with highest forest regeneration potential. Finally, we provide indicators that can be used to identify native tree species with higher potential for restoration of degraded lands.

REGENERATION BOTTLENECKS FOR COLONIZING SPECIES

Different biophysical factors determine the transition probabilities of colonizing species from the seed stage to later life-cycle stages in abandoned agricultural fields (Dalling & Denslow 1998, Dalling *et al.* 2002, Arroyo-Rodríguez *et al.* 2015, Lu *et al.* 2016). Demographic studies can help to explore how propagule availability and biophysical variables, after abandonment, determine the probability of a seed to become a mature plant for different pioneer species. Here, we use demographic data, encompassing all life-cycle stages, for three typical pioneer tree species from southern Mexico, to explore regenerative bottlenecks these trees endure during the first 3 years after the abandonment of a cornfield (see *Methods* in Appendix S1).

On an annual basis, seed rain and soil seed bank were abundant for all three species (Fig. 2), especially for *Trema micrantha*, indicating that dispersal limitation, and propagule availability in general, was not a bottleneck. However, important differences in seed biology among species suggest that an increase in the harshness of agricultural land use may have different consequences for regeneration of these species. Seeds of *Trema* and *Cecropia obstusifolia* are small, copiously and continuously produced

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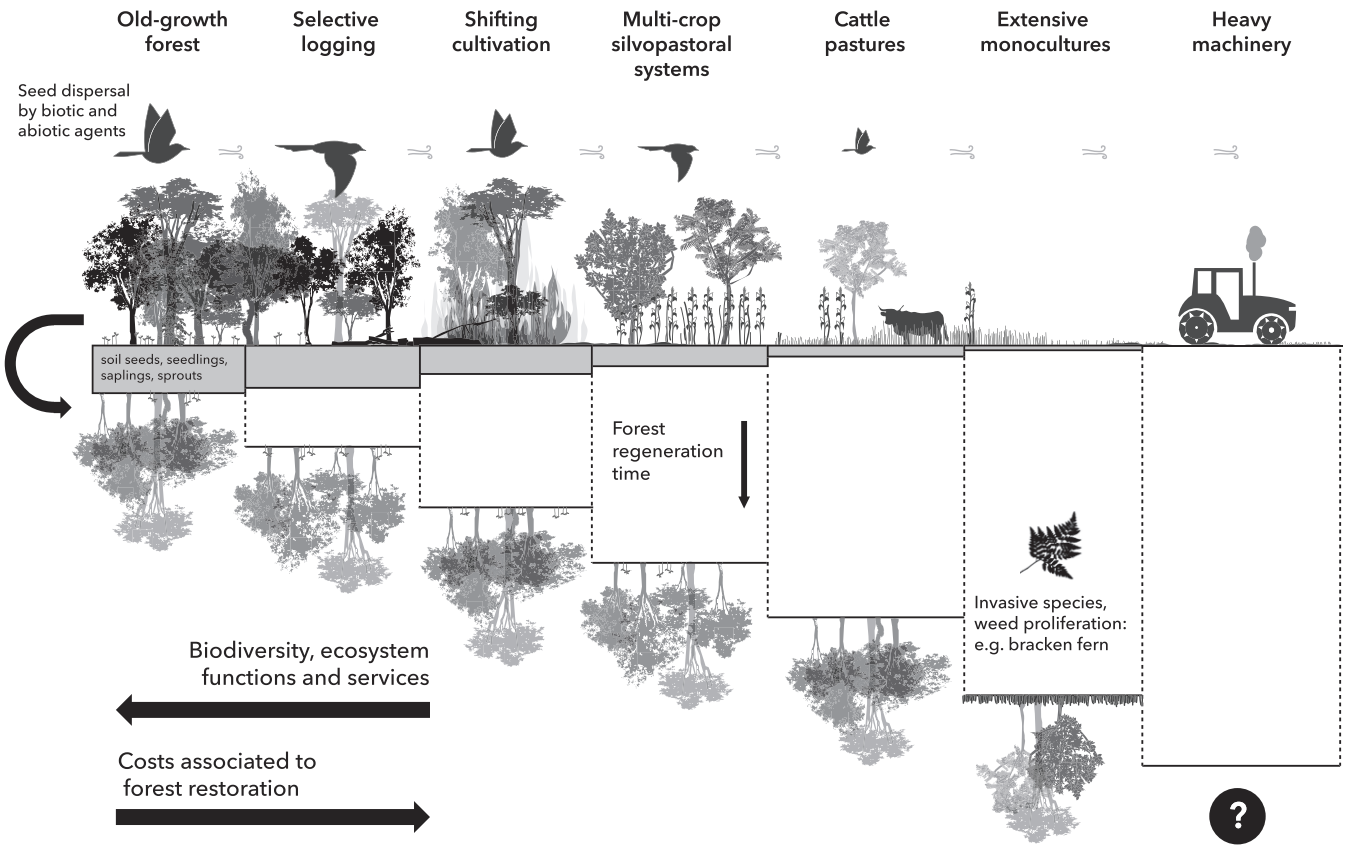

FIGURE 1. Conceptual drawing illustrating agricultural land use effects on forest regeneration potential. Under mild land uses, such as selective logging or shifting cultivation, propagule availability (soil seeds, and seedling, sapling and re-sprout banks), seed rain (coming from external seed sources via animal seed dispersers and wind), and biophysical factors after field abandonment do not represent barriers for forest regeneration. As size, duration, and severity of disturbance inflicted by agriculture land uses increases (see first horizontal arrow) forest regeneration potential decreases (and time for forest recovery become longer; indicated by the vertical arrow and the length of the discontinuous lines) and forest structure and composition change respect to pre-disturbance ones. Under extreme disturbance conditions the field can be invaded by weeds, natural forest regeneration is unlikely (uncertain time of recovery), and active restoration actions are needed. With increasing agricultural disturbance dispersal limitation intensifies (mostly by the loss of biotic seed dispersal, indicated by the decrease in the size of the bird image; symbol in front of birds represent wind) and establishment limitation increases, and biodiversity, ecosystem functions and services of regenerating forests decline, while the costs required for restoration increase. Modified from García-Orth (2008).

(Álvarez-Buylla & Martínez-Ramos 1990), and dispersed by a rich array of highly mobile vertebrates (Estrada *et al.* 1984). In contrast, the larger seeds of *Trichospermum mexicanum* are wind-dispersed, and produced only during the dry season (Ibarra-Manriquez *et al.* 1991). These reproductive differences partially explain why the year around abundance of seeds was over one order of magnitude smaller in *Trichospermum* than in the other two species. *Trichospermum* seeds were 30 times more abundant in soil than in the seed rain, suggesting a long-lasting seed bank. In contrast, *Trema*'s seed rain was far more abundant than soil seeds, suggesting these seeds do not accumulate in the soil. In *Cecropia* seed rain and soil seed abundances were similar, also suggesting no seed accumulation. In old growth forest sites, *Cecropia* soil seeds have very short lifespans (<10 days), suffering high predation rates by insects and pathogens; they are dynamically replaced by newly and abundant dispersed seeds (Álvarez-Buylla & Martínez-Ramos 1990). Also, in recently abandoned cornfields (Corzo-Domínguez 2007) and pastures (García-Orth & Martínez-Ramos 2008) *Cecropia* soil seeds suffered predation rates close to 100 percent within few days. While *Trema* has similar seed population dynamics, *Trichospermum* may be much better in resisting predation and diseases. In terms of our conceptual framework (Fig. 1), regeneration potential of pioneer species like *Cecropia* and *Trema* would be more sensitive to extensive (*i.e.,* large-sized) agricultural land uses (*e.g.*, cattle pastures or monocultures of several dozen hectares; Fig. 1), which reduce animal seed dispersal, while species like *Trichospermum* could be more sensitive to severe land uses (*i.e.,* those causing high *in situ* environmental modification; Fig. 1) that reduce or eliminate the soil seed bank.

Two years after field abandonment, *Cecropia* was the only species with seedlings (Fig. 2A) indicating strong establishment limitations for *Trema* and *Trichospermum*. Likely, as soon as colonizing vegetation forms a closed canopy cover, and light availability declines in the understory, seeds of these two pioneer trees

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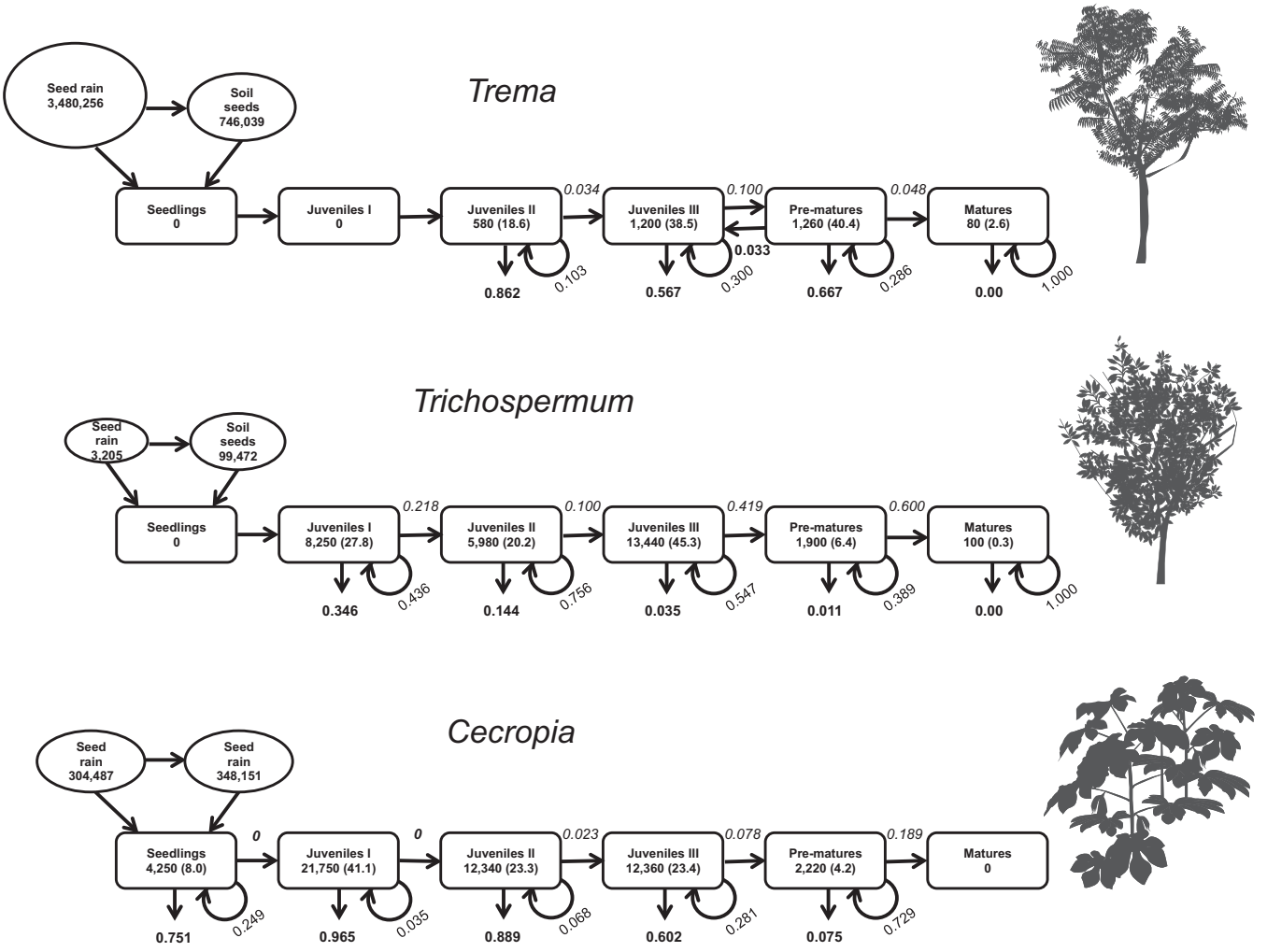

FIGURE 2. Diagrammatic life-table of the three dominant pioneer tree species studied in an abandoned cornfield (1.5 years fallow age) in Marqués de Comillas, southern Mexico. Propagule availability is illustrated in ellipses, whose size is related with the density of soil seeds and dispersed seeds (seed rain) per hectare. Rectangles show density (individuals per hectare) of trees in life-cycle categories: Seedlings (<50 cm height), Juveniles I (50 to 150 cm height), Juveniles II (151 cm tall to 2.5 cm DBH), Juveniles III (2.6 to 5 cm DBH), Pre-matures (5.1 to 10 cm DBH) and Matures (>10 cm DBH). In these categories, for a time period of 1 year, right-headed horizontal arrows represent progression from one to the next stage, left-headed horizontal arrows represent reduction in size due to broken stems, circle arrows indicate same-stage persistence and vertical arrows indicate mortality. Numbers between stages indicate annual progression or retrogression rates (ind/ind/yr), annual mortality rates (ind/ind/yr) at the tip of vertical arrows and annual permanence rates (ind/ind/yr) aside circle arrows. Transition rates between seed rain and soils seeds, as well as between these stages and newborn seedlings are unknown.

were unable to germinate and/or newborn seedlings died soon after emergence. *Trema* and *Trichospermum* were less shade-tolerant than *Cecropia*, and probably prosper better in large open fields. For *Trema*, this was confirmed in Barro Colorado Island where this tree requires larger gaps than *Cecropia* to regenerate (Brokaw 1987). *Trichospermum* could be intermediate as indicated by the fact that this species exhibited a middle density of juvenile trees between *Trema* and *Cecropia* in our abandoned cornfields (Fig. 2). The abundant seedlings and saplings of *Cecropia*, however, suffered high mortality rates (>60% per year) and only 2.3 percent of the juveniles-1 (50–150 cm height) reached sizes larger than 1 cm dbh over the studied year (Fig. 2). In contrast, *Trichospermum* exhibited lower mortality and higher progression rates in the juvenile stages, increasing its survival and growth as individuals transited to further life-cycle stages. *Trema* exhibited high mortality and low progression rates in juvenile and pre-mature stages (4.1–8 cm dbh). These results are indicative of the strong competition that pioneer trees endure during the first years of old-field succession (van Breugel *et al.* 2012), and likely indicate differences in the ability of the species to use light resources and to cope with natural enemies (herbivores and diseases) in juvenile and pre-mature stages. In the three species, mortality decreased and growth increased markedly in the mature stage, when treecrowns get exposed to direct sunlight.

As a net result of these demographic transitions and ecological filters, *Trichospermum* recruited more mature trees than *Trema* and *Cecropia*, which reached mature sizes only three years after field abandonment. Most individuals (40%) in the *Trema* population were in the pre-mature stage (4.1–8 cm dbh), most of *Trichospermum* (45.3%) in the Juvenile-III stage (2.1–4 cm dbh) and most of the *Cecropia* (41.1%) in the Juvenile-I stage (51–150 cm height; Fig. 2). Such differences in population structure suggest that *Trema* was the first colonizer, followed by *Trichospermum* and then by *Cecropia*. However, if all species colonized the field at the same time, differences in inter-specific growth and mortality rates due to, for example, competition and diseases, may also generate such contrasting demographic structures (van Breugel *et al.* 2007, 2012). Indeed, detailed demographic studies are needed to assess the recruitment rate and colonization sequence of pioneer trees, like those studied here. These processes would change under the effects of disturbance caused by different agricultural land uses on propagule availability (*i.e.*, dispersal limitation) and the biophysical environment (*i.e.*, establishment limitation). Lacking such demographic details, the following section addresses this issue using a community ecology approach.

EFFECTS OF LAND USE LEGACIES ON FOREST REGENERATION

Agricultural land use types may differ widely in variables such as size of the agricultural field, years of use, harvest frequency, type of machinery and tools used, fire frequency and intensity, amount and frequency of agrochemicals, biomass and aggressiveness of exotic species, and density of livestock (Zermeño-Hernández *et al.* 2015). The legacies of different agriculture land uses, therefore, will reflect in the structural, compositional, functional, and dynamic attributes of regenerating forests (Levy-Tacher & Aguirre-Rivera 2005, Chazdon 2014, Mesquita *et al.* 2015).

Regeneration Effects of Two Contrasting Agricultural Land Uses.—In Marqués de Comillas, southeastern Mexico, we compared forest regeneration dynamics in abandoned cornfields (van Breugel *et al.* 2006, 2007) and cattle pastures, which are the dominant agricultural land uses in that region (Zermeño-Hernández & Martínez-Ramos 2016) and in many HMLs throughout Mesoamerica. Pastures were larger in size, more severe (including burning events) in agricultural practices and longer lasting than cornfields (Tables S1 & S2), but were located within the same geomorphology unit and landscape matrix (see *Methods* Appendix S2).

Six years after the abandonment of the study fields, shrub and tree assemblages (height >1 m) in the pastures were 2–15 times lower in stem density, basal area (a surrogate for aboveground biomass), plant maximum height, and species density than in the cornfields (Table 1). While the cornfield regenerating forests were richer in species and higher in biomass, thus providing superior carbon storage and sequestration than those in the pastures, rarified species richness and species diversity (rarefied or not) of secondary forests in cornfields and pastures were similar (Table 1). Under the better environment conditions in cornfields, a few dominant pioneer species rapidly monopolized the resources and grew very fast, outcompeting other species which represented only a small fraction of basal area in the canopy and understory (three species covering 60 percent of basal area; Fig. S1A). The harsher environment prevailing in the pastures after abandonment (Zermeño-Hernández *et al.* 2015) was a barrier for highly competitive species, resulting in a more even species representation (six species covering 60 percent; Fig. S1A). In addition, the abandoned cornfields and pastures were colonized by assemblages with different species composition: a species similarity analysis, using a species basal area based Bray-Curtis index, showed that secondary forests in fields with different land use (cornfield-pasture; mean similarity = 3.6%) were 4–7 times less similar than those in fields with same land use (cornfield-cornfield = 28.2%; pasture-pasture = 15.3%), and a non-metric multidimensional scaling analysis fully separated cornfields from pastures along the main ordination axis (Fig. S1B). While typical pioneer trees colonizing canopy gaps in old growth forest (such as *Trichospermum*, *Ochroma*, *Helicarpus*, and *Piper*) dominated the cornfields, species related to savanna-like vegetation (*e.g., Byrsonima crassifolia*, *Curatella americana* and *Vismia camparaguey*) dominated the pastures (Fig. S1A).

Similar legacies of agricultural land uses were found in a long-term study that contrasted successional forest pathways between abandoned clearcuts, which represented a relative mild land use, and cattle pastures, which represented a harsh land use (including multi-episodes of burning), in Manaus, Brazil (Mesquita *et al.* 2015). Twenty-five years after abandoned, diverse and structurally complex second growth forests developed in the clearcuts while structurally simple and low diverse ones developed in the pastures. Another example is in regenerating forest near Tefé, Brazil, where swidden agriculture land use intensity also reduced regeneration and impacted the regenerating community (Jakovac *et al.* 2015). These studies strongly support the

TABLE 1. *Mean (±SE) values of structural attributes of regenerating forests 6 years after the abandonment of cornfields (*N *= 3) and cattle pastures (*N *= 2) in Marques de Comillas, Southeastern Mexico. For each attribute, land uses not sharing same letter are significantly different (*P *< 0.05, Generalized Liner Models).*

	Land use	
Attribute	Cornfield	Pasture
Stem density (stems/500 m^2)	680.0 ± 227.5[a]	56.7 ± 2.0[b]
Basal area (m^2/500 m^2)	0.90 ± 0.14[a]	0.06 ± 0.01[b]
Mean maximum height (m)	12.9 ± 0.6[a]	7.3 ± 0.8[b]
Species density (species/500 m^2)	54.0 ± 5.8[a]	25.0 ± 2.0[b]
Rarified species richness (species/57 stems)	20.1 ± 3.0[a]	20.7 ± 0.3[a]
Species diversity (dominant species/500 m^2, D)	3.4 ± 1.2[a]	5.1 ± 1.1[a]
Rarified species diversity (D/57 stems)	3.2 ± 1.0[a]	4.9 ± 0.9[a]

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hypothesis that forest regeneration rate (gain in species diversity and biomass per unit of time and space) is reduced with the harshness of the land use, especially when recurrent burning occurs, and that contrasting agricultural land uses may lead to divergent successional pathways.

Assessing regeneration effects in agricultural land use gradients.—As different agricultural land uses occur at the same time in HMLs, their joint impact on forest regeneration potential needs to be assessed (*e.g.,* Pascarella *et al.* 2000, Holl 2007). To predict forest regeneration potential in any abandoned agricultural field in a complex multi-land use HML we constructed a simple index based on information provided by landowners and farmers (Zermeño-Hernández *et al.* 2015). Our Ecological Disturbance Index (*EDI*) was derived from the analysis of agricultural land uses as ecological disturbance regimes (*sensu* Pickett & White 1985). *EDI* incorporates, in an additive way, three major disturbance components: size (field area in hectares), duration (years of agricultural use) and severity (including fire incidence, chemical use, machinery use, stocking rate, and tree cover in the field; see Appendix S3). The index varies from 0 (no disturbance) to 3 (maximum disturbance; Zermeño-Hernández *et al.* 2015).

We tested EDI's usefulness to predict forest regeneration potential in an experiment in Marqués de Comillas (see Appendix S4), where forest regeneration was monitored in recently abandoned fields differing widely in *EDI* values. Plant density, species density, and above ground biomass of shrubs, trees and lianas (10–150 cm height) were quantified at the time of field abandonment and 2 years later, in permanent plots near (<5 m) and far (>100 m) from nearest forest remnants. Regeneration rates for abundance, species density, and species diversity decayed exponentially with *EDI* (Zermeño-Hernández *et al.* 2015). In contrast, physiochemical soil variables measured at the time of abandonment (for details, see Zermeño-Hernández *et al.* 2015) failed to explain the among field variation in regeneration rates. Only microclimate variables such as air temperature, relative humidity, and vapor pressure deficit predicted regeneration rates. To our surprise, the farmer-based simple and cheap-to-get *EDI* index indicated the recovery of abundance, species density and diversity as well as measurements of microclimate conditions, which are costly (*e.g.*, equipment requirement) and time consuming, especially when rapid assessment of many agricultural fields is required.

Dispersal limitation plays an important role in forest regeneration potential (Reid *et al.* 2015). Plant density and diversity decreased significantly with *EDI* only near edges of forest remnants (Fig. S2), implying that severe and long-lasting agricultural land use strongly limits forest regeneration even under abundant seed rain (I. Zermeño-Hernández pers. obs.). In contrast, the lack of EDI impact far from forest edges (Fig. S2) indicates that both dispersal limitation and harsh environmental conditions constitute important barriers for regeneration.

Contrary to abundance and diversity of regenerating forests, aboveground biomass (AGB) did not change with *EDI*. Instead, biomass of 2-year-old regenerated vegetation was positively related with light availability at the time of abandonment (Zermeño-Hernández *et al.* 2015). Cornfields and pastures had higher levels of light availability than cacao plantations and few pioneer species dominated the regenerating vegetation under the high light conditions. Also, we found that AGB was negatively related with soil nitrogen content; maybe the high nitrogen demand of the fast growing pioneer trees strongly decreased soil nitrogen (Bazzaz & Pickett 1980), promoting N fixing trees in early succession (Batterman *et al.* 2013, Menge & Chazdon 2016). Thus, while EDI components (size, duration, and severity) were good indicators of propagule availability, and hence of the abundance and diversity of regenerating plant communities, soil and microclimatic conditions at the time of abandonment were better indicators of plant performance (Zermeño-Hernández *et al.* 2015).

Scaling *EDI* at the landscape level.—Depending on land-use history, socioeconomic factors (*e.g.*, years since human colonization, agrarian policies, economy) and biophysical variables (*e.g.*, topography, soil quality), the land covered by old growth forest fragments and different agricultural land uses may vary widely among HMLs. Conceptually, it can be expected that the extent and ecological properties of second growth forests in such landscapes may depend on the extent of the old growth forest remnants (*i.e.*, size of seed pools) and the disturbance regimes imposed by the different agricultural land uses (affecting *in situ* propagule availability and environmental conditions in the abandoned fields). However, the cumulative impact of disturbance, caused by different land uses occurring in a landscape, on the ecological properties of second growth forest still needs to be assessed (Chazdon 2014).

We developed the *EDI*-based Ecological Disturbance Landscape Index (EDI_L, Zermeño-Hernández & Martínez-Ramos 2016) for this purpose and tested the hypothesis that structural attributes (stem density, species density, species diversity, and biomass) of second growth forests are reduced with increasing disturbance regimes, associated with the mosaic of land uses in the landscape. EDI_L is calculated as $EDI_L = EDI_i * p_i$, where EDI_i is the average *EDI* value for all fields with land use type *i*, and p_i is the cover proportion of that land use type in the landscape. We tested the usefulness of this index in a study in Marqués de Comillas. To quantitate EDI_i for different agricultural land uses, Zermeño-Hernández and Martínez-Ramos (2016) did semi-structured interviews with 68 owners of 156 agricultural fields encompassing 13 different agricultural land uses. The EDI_i values ranged from 0.60 to 0.75 for agroforestry systems (*e.g.*, coffee, orchard, cocoa plantations) from 1.3 to 1.5 to 1.9 monocultures (*e.g.*, cornfields, bean and rice fields) and was 1.9 for extensive farming (*e.g.*, pastures, oil palm plantations). We incorporated in EDI_L the proportion of area occupied by old growth forest remnants ($EDI = 0$), and of patches of secondary vegetation ($EDI = 0.25$), considering that old growth forest represent the undisturbed condition and that secondary forests may attain important levels of biodiversity and biomass, as documented for other studies conducted in Marqués de Comillas (van Breugel

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et al. 2006, 2007, Lohbeck *et al.* 2014, 2016) and in other Neotropical regions (Norden *et al.* 2015, Poorter *et al.* 2015, 2016). This value, however, is tentative because *EDI* of secondary forests may change from a relatively high starting value, defined by the disturbance regime imposed by the agricultural land use before abandonment (Mesquita *et al.* 2015, Zermeño-Hernández *et al.* 2015) to a value of 0, if the secondary forest, over time, reaches a structure and function similar to that of the old growth forest.

Our study system consisted of ten landscapes (1-km^2 each) for which EDI_L values, as well as different structural community attributes and fallow age (years) of second growth forests, were quantified (see Appendix S5). Overall, tree density did not change with EDI_L but species density ($R^2 = 0.58$, $P < 0.01$), basal area ($R^2 = 0.92$, $P < 0.01$), and species diversity (Inverse Simpson index, $R^2 = 0.45$, $P = 0.03$), decreased with EDI_L (Zermeño-Hernández & Martínez-Ramos 2016). As these tree community attributes tend to increase with second growth forest age (Norden *et al.* 2015), and landscapes with low EDI_L values (*i.e.*, recently opened to agriculture) could have younger forests than landscape with high EDI_L values, we checked that EDI_L effects were independent of forest age. For this, we obtained the mean fallow age of secondary forests recorded in each landscape. Indeed, across landscapes mean structural attribute values of secondary forests varied independently of mean fallow age (regression analysis, $N = 9$, $P > 0.10$).

In our studied landscapes, EDI_L was largely determined by the percentage of land covered by cattle pastures (%CP), which had the higher *EDI* value (Zermeño-Hernández & Martínez-Ramos 2016). Pastures covered between 7 and 93 percent of the studied landscapes, and represented between 71 and 100 percent of the land covered by agriculture. Therefore, we expected that %CP in the landscape could be a simpler indicator of the second growth forest attributes. Indeed, species density, species diversity, and basal area declined with %CP across landscapes (Figs. 3A–C). We also expected that the values of the regenerating forest attributes would increase with the percentage of the landscape covered by old growth forest remnants (%COF), because more forest should imply greater species availability to colonize the abandoned fields. This expectation was supported by our results as basal area, and to a lesser degree species density and species diversity, increased with %COF (Figs. 3D–F). In fact, %CP was a stronger indicator of regenerating forest attributes (higher R^2 in relationships shown in Fig. 3) than %COF. Whether this result indicates that severity and duration of agricultural land uses (represented by %CP) were more important than availability of seed sources in the landscape (represented by %COF) for forest regeneration needs further exploration. That %CP was closely related to EDI_L ($R^2 = 0.91$, linear regression) indicates that this simple and inexpensive landscape metric (quantified with satellite images and GIS) can be employed to predict average second growth forest attributes at the landscape level. However, because EDI_L integrates in a single index the disturbance regime effects inflicted by different land uses in a landscape, this index is not useful to predict forest regeneration potential on a single abandoned field.

In summary, our findings indicate that: (1) ecological quality (density, species diversity, biomass) of second growth forests systematically decreases with high area of land uses that lead to severe landscape disturbance (*e.g.*, extensive cattle pastures); and (2) it is imperative to preserve high coverage levels of old growth forests in the landscape to assure regeneration of high ecological quality second growth forests. Therefore, in designing HMLs where second growth forests contribute importantly to conserve biodiversity, it is mandatory to establish low impact agricultural land uses embedded in a matrix of both second growth and old growth forest.

MAXIMIZING THE SUCCESS OF LARGE-SCALE NATURAL REGENERATION AND RESTORATION

In extremely disturbed abandoned fields, natural regeneration is limited by a series of biotic and abiotic barriers (Aide & Cavelier 1994, Hooper *et al.* 2005, Fig. 1) and identifying and removing such barriers is critical for forest recovery. Two major barriers are the lack of propagules due to dispersal limitation (Holl 1999), and the competition/interference exerted by exotic or weed plants (Caterall 2016). A way to overcome dispersal limitation is sowing seeds of native plant species that can foster forest recovery (Cole *et al.* 2011). However, with frequency sown seeds suffer high predation rates and protection from invertebrate and vertebrate granivores is needed. For example, in Marqués de Comillas, sowed seeds in abandoned cattle pastures of the pioneer trees *Cecropia obtusifolia* (Cecropiaceae) and *Ochroma pyramidale* (Malvaceae) suffered 100 percent removal in only 8 days (mostly by ants), and those of the late-successional trees *Brosimum alicastrum* (Moraceae) and *Dialium guyanense* (Leguminosae) suffered 80–100 percent removal rates by ants and rodents in 64 days (García-Orth & Martínez-Ramos 2008). Except *Cecropia* (whose seeds all die), only when sown seeds were protected from granivores (using a small cage of metallic mesh and buried) they produced seedlings, and even then emergence seedling level was low (7–12% across species). In recently abandoned cornfields, the exclusion of vertebrate granivores (using small cages of metallic mesh) reduced removal rates of sown seeds of eight pioneer and late-successional tree species in 38–65 percent, and increased seedling emergence in 7–35 percent (Corzo-Domínguez 2007). Thus, removing the barrier imposed by seed predators must follow overcoming dispersal limitation by sowing seeds.

Once the seedlings have emerged they face other biotic and abiotic barriers before reaching the juvenile and mature stages (Arroyo-Rodríguez *et al.* 2015). For example, in abandoned pastures exotic grasses may exert strong competition/interference on emerged seedlings (Holl *et al.* 2000, Hooper *et al.* 2005, Celis & Jose 2011). Grass removal enhanced survival and growth of seedlings, fostering forest regeneration (Holl *et al.* 2000, Meli *et al.* 2015), under the condition of sufficient regenerative propagule availability. A grass removal experiment we conducted in Marqués de Comillas exemplifies the combined effects of dispersal limitation (*i.e.* distance to nearest forest fragment) and grass vegetation

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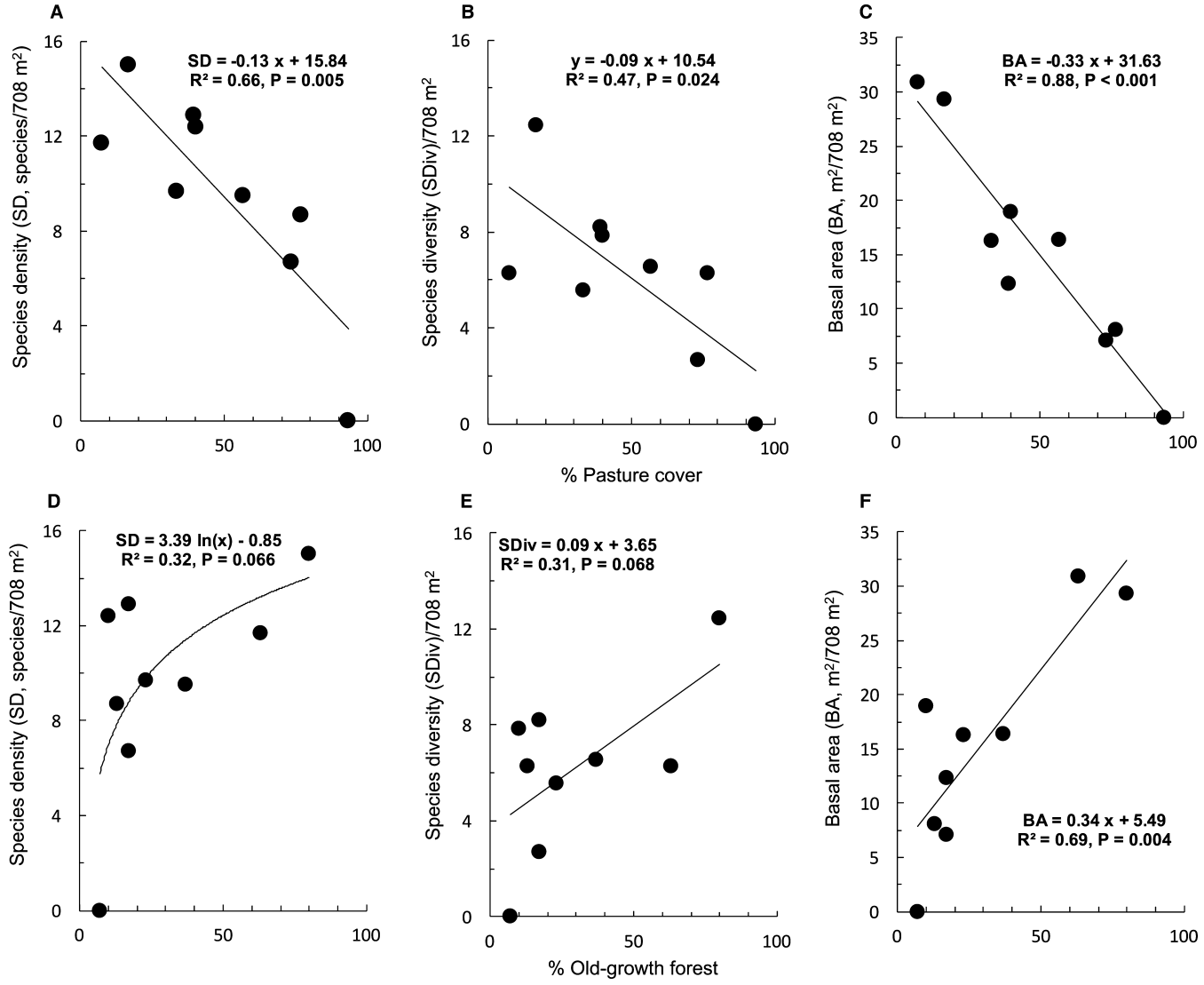

FIGURE 3. Relationships between structural attributes (species density, species diversity and species diversity) of second growth forests and the percentage of the landscape covered by cattle pastures (A, B, C), and the percentage covered by old growth forest remnants (D, E, F) in Marqués de Comillas, southern Mexico. Each dot represents a landscape of 3 × 3 km. In each panel, the best general linear model (GLM) and its statistical significance are shown. For species density and species diversity (calculated with the inverse of Simpson diversity index, measuring the effective number of dominant species) in the GLM, we used a Poisson error and an identical link function while for basal area a normal error and an identical link function was used.

(*i.e.* establishment limitation) as forest regeneration barriers. In two pastures close (<500 m) and two pastures far (>1000 m) from nearest forest remnants, grass removal effects were assessed 3.5 years after abandonment considering plant density, species density, and basal area of regenerating forests (shrubs and trees ≥ 1 m height; see Appendix S6). Forest attribute values of all woody plants together were significantly higher in plots close to forest remnants than far away, and grass removal increased only basal area in the close plots (Table 2). Only trees, however, responded in all attributes both to distance and grass removal; close to forest remnants, where trees were dominant, grass removal significantly increased all forest attributes, but far away in shrub-dominated plots, grass removal had no effect on trees (Table 2). These results support the view that forest regeneration is especially affected by dispersal limitation and that elimination of the grass barrier can improve forest recovery, if seed sources are close (Holl *et al.* 2000, Benitez-Malvido *et al.* 2001, Hooper *et al.* 2005).

Transplanting seedlings of native species may assist forest recovery in degraded lands (*e.g.*, Román-Dañobeytia *et al.* 2012, Gilman *et al.* 2016). Because performance of transplanted seedling varies widely depending on species' attributes (Martínez-Garza *et al.* 2013, Douterlungne *et al.* 2015) and environmental conditions in the transplanting site, intensive human care is highly needed. Propagation of seedlings in nurseries and caring the transplanted seedlings in the field implies important economic

TABLE 2. *Mean (±SE) values of structural attributes of regenerating forests 3.5 years after abandonment of cattle pastures, located close (< 500 m, N = 2) and far away (> 1000 m, N = 2) from nearest forest remnants, with grass vegetation (G) and removing grass vegetation (GR), in Marqués de Comillas, Southeastern Mexico. Values are provided separating shrubs from trees, and combining all plants (height ≥ 1 m). Plant density is given in plants/750 m^2, species density in species/750 m^2, and basal area in m^2/750 m^2; for each treatment, percentage contribution of shrubs and trees to total value of each attribute is given in parenthesis. For each plant group and attribute, treatments not sharing same letter are significantly different (P < 0.05, Generalized Linear Models); for count variables (plant density and species density) a Poisson error and a log-link function was used while for basal area a normal error and an identical link function was used.*

Plant group	Close		Far	
Trees	G	GR	G	GR
Plant density	63.0 ± 8.0^{b} (49.8)	88.5 ± 4.5^{c} (61.0)	18.5 ± 12.5^{a} (33.9)	9.5 ± 8.5^{a} (18.1)
Species density	17.5 ± 0.5^{b} (58.3)	23.5 ± 3.5^{bc} (58.0)	9.0 ± 4.0^{ab} (41.9)	5.0 ± 4.0^{a} (29.4)
Basal area	0.034 ± 0.002^{b} (57.6)	0.069 ± 0.001^{c} (67.4)	0.005 ± 0.003^{a} (24.8)	0.009 ± 0.009^{a} (44.7)
Shrubs				
Plant density	63.5 ± 3.5^{a} (50.2)	57.0 ± 18.0^{a} (39.0)	36.0 ± 14.0^{a} (66.1)	43.0 ± 17.0^{a} (81.9)
Species density	12.5 ± 0.5^{a} (41.7)	17.0 ± 2.0^{a} (42.0)	12.5 ± 1.5^{a} (58.1)	12.0 ± 2.0^{a} (70.6)
Basal area	0.025 ± 0.018^{a} (42.4)	0.033 ± 0.012^{a} (32.6)	0.014 ± 0.005^{a} (75.2)	0.010 ± 0.007^{a} (55.3)
All plants				
Plant density	126.5 ± 11.5^{a}	145.5 ± 13.0^{a}	54.5 ± 26.5^{a}	52.5 ± 25.5^{a}
Species density	30.0 ± 0.0^{ab}	40.5 ± 5.5^{b}	21.5 ± 5.5^{ab}	17.0 ± 6.0^{a}
Basal area	0.059 ± 0.017^{b}	0.102 ± 0.011^{c}	0.019 ± 0.008^{a}	0.019 ± 0.015^{a}

investments, especially in large-scale reforestation programs. Therefore, assessing which tree species are the best (*i.e.,* high survival and growth with low investment) for restoration is crucial (Caterall 2016).

We developed a Species Selection Index (*SSI*; Martínez-Ramos & García-Orth 2007, Fuentealba & Martínez-Ramos 2014) to aid in the selection of species useful for restoration, particularly when resource availability for restoration is low (*e.g.*, non-automated tree nurseries are available). As described in Appendix S7, *SSI* < 1 indicate best species for restoration, *i.e.*, those whose transplanted seedlings perform well with and without care. Here, we apply *SSI* to restoration of fields covered by bracken fern (*Pteridium aquilinum*) in Marqués de Comillas, where it grows abundantly in degraded pastures (Suazo *et al.* 2015). The fern forms dense mono-specific patches impeding natural forest regeneration, and different ways have been explored to remove this shade-intolerant weed (*e.g.*, Douterlungne *et al.* 2010), including transplanting tree species to produce shade (Douterlungne *et al.* 2013). We used *SSI* to identify potential tree species able to survive and grow in the presence or absence of the fern cover (see *Methods* in Appendix S7); in total, we tested six species. Eight months after transplantation only *Ochroma pyramidale* seedlings had higher survival in the presence than in absence of the ferns (Fig. 4A). Height growth rate was higher in the absence of fern in five species, but *Ochroma* grew faster in the presence of fern (Fig. 4B). The *SSI* index showed *Ochroma* (performing well in fern presence), *Cojoba arborea* and *Tabebuia guayacan* (well in fern absence) to be the best species for restoration and *Cedrela odorata* and *Brosimum alicastrum* the worst (Fig. 4C). *Ochroma* seedlings need no care, drastically reducing restoration cost. In fact, local people use this tree to reduce cover of bracken fern in infested (Levy-Tacher *et al.* 2015). Future studies need to address why *Ochroma* survives and grows better in the presence of bracken fern. For now, we noted that species having *SSI* < 1 had leaf area gains in the presence of fern while species with *SSI* > 1 had leaf area losses (data not shown). This suggests that species having high morpho-physiological plasticity could perform well for restoring degraded fields as shown in other studies (Martínez-Garza *et al.* 2005, 2013).

Of course, even species that require high economic investment for improving their performance in the degraded site can be selected to recover desirable ecosystem functions and services and to increase species and functional diversity of the restoring vegetation. A limitation of *SSI* is that pilot studies are needed to assess seedling performance with and without care, requiring additional and sometimes high resource investment. The *SSI* index can be improved by considering the net present and future value of transplanting seedlings. For example, as time passes the initial investment decreases (depending, among other things, on inflation rates) while future value can increase if the transplanted species offer valuable uses (*e.g.*, fruits, timber, fire-wood, fodder for cattle). The incorporation of societal criteria for selecting native tree species for restoration would also increase the usefulness of the *SSI* index (Meli *et al.* 2014).

CONCLUDING REMARKS

This review shows important guidelines for maintaining forest regeneration potential in HMLs. First, at the field (local) scale, this potential is enhanced as the size, duration, and disturbance severity of the agricultural land use decline and the regeneration bottlenecks become weaker. Agricultural land uses maintaining high levels of tree cover, minimizing the use of fire, agrochemicals, and heavy machinery, and having short-use periods, allow

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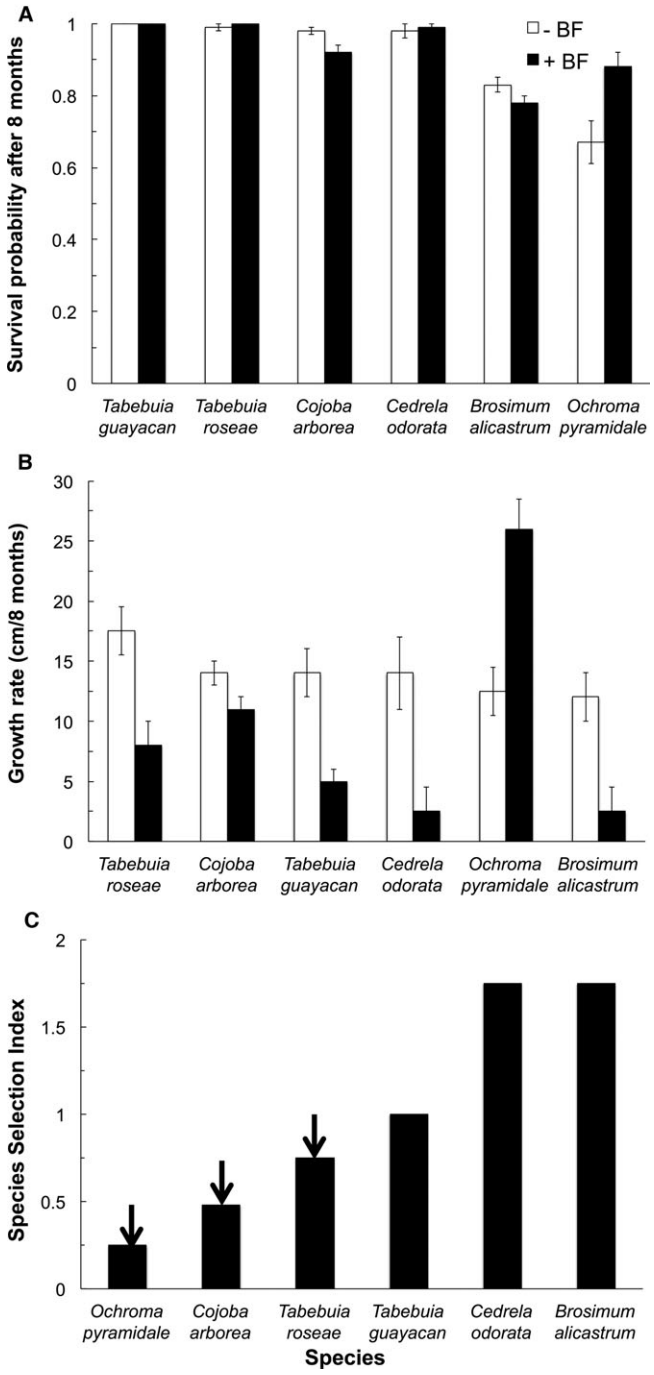

FIGURE 4. Survivorship, growth, and Species Selection Index (*SSI*) of seedlings of six tropical forest species transplanted into an abandoned pasture field covered by bracken fern (*Pteridium aquilinum*) in Marqués de Comillas, southern Mexico. (A) Survivorship of seedlings 8 months after transplantation under the presence (+BF) and removal of the aboveground fern tissues (−BF); the removal of such tissues was repeated every 2 months to control fern regrowth. (B) Absolute growth rate of seedlings after 8 months of transplantation under +BF and –BF treatments. In (A) and (B) panels, vertical lines indicate one standard error. (C) *SSI* values for the six transplanting species 6 months after transplantation; arrows indicate the species more recommendable for restoration of pastures covered by bracken fern in the study site.

forest regeneration best. Diverse agroforestry and agro-ecological systems (Schroth *et al.* 2004, Bhagwat *et al.* 2008, Perfecto & Vandermeer 2008), and those preserving remnant trees of native species, which function as regeneration nuclei (Guevara *et al.* 1986, Harvey & Haber 1998, Schlawin & Zahawi 2008, Derroire *et al.* 2016), represent examples of such land uses. Second, at the landscape scale, the ecological quality (*e.g.*, high species diversity and biomass) of regenerating forest increases with the extent of old growth forest remaining in the landscape, which function as major source of species in the regeneration process at the field scale (Lu *et al.* 2016). A promising composition of HMLs where agricultural production and biodiversity conservation can be conciliated is a mosaic of agroforestry and agro-ecological systems imbedded in a matrix of old growth and second growth forests (Chazdon & Uriarte 2016). Agricultural fields must retain forest cover in their vicinity (*e.g.*, live fences and other living structures acting as biological corridors) to facilitate the movement of pollinators, seed dispersers, herbivores, and other animals playing key roles in forest regeneration (Omeja *et al.* 2016). The area devoted to second growth forests would be retained for long time periods, as biodiversity and ecosystem functions and services of these forests increase with forest age (Chazdon 2014); enriching secondary forests with species providing valuable timber and non timber forests products, and developing sustainable and economically viable forest management programs for landowners, could help to reach this objective (Lamb *et al.* 2005, Chazdon *et al.* 2009, Gilman *et al.* 2016). Ideally forest regeneration would be promoted at the boundaries of old growth forest fragments, especially the small ones, to buffer edge effects and promote forest connectivity across the landscape. Conserving high levels of forest cover in HMLs also promotes preservation of native fauna, including large vertebrates (*e.g.*, Banks-Leite *et al.* 2014, Muench & Martínez-Ramos 2016, Omeja *et al.* 2016) that play important ecological roles (as pollinators, seed dispersers, controllers/regulators of diseases, among other functions) in forest regeneration and maintenance of biodiversity in the landscape (Dirzo *et al.* 2014, Latawiec *et al.* 2016).

Presently, in most HMLs just one or few extensive agricultural land uses (*e.g.*, large pastures, conventional soy fields, commercial tree/palm plantations), often promoted by governmental or private incentives, tend to dominate. It is an extraordinary challenge to change this monodominant land use trend into the diverse mosaic described above, as this depends on a complex suite of societal and ecological factors (Adams *et al.* 2016, Lazos *et al.* 2016, De Souza *et al.* 2016). Modifying present agricultural practices is critical for encouraging socially and environmentally accepted sustainable systems (Castillo & Toledo 2000, Perfecto & Vandermeer 2008, Strassburg *et al.* 2016). Future dynamical landscape studies would adopt socio-ecological, transdisciplinary, approaches with the participation of key stakeholders, to look for alternative landscape managing strategies (*e.g.*, land sharing versus land sparing; Phalan *et al.* 2011, Uriarte & Chazdon 2016), and assessing the feasibility of transforming the landscape into a diverse mosaic in which biodiversity and human livelihoods can be balanced (Chazdon & Uriarte 2016, Mukul *et al.* 2016).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Methods used to obtain demographic rates.

Appendix S2. Further description of the sites and methods used to assess the effects of contrasting agricultural land uses.

Appendix S3. Procedure followed to construct the Ecological Disturbance Index (*EDI*).

Appendix S4. Experimental system used to test the predictive ability of the Ecological Disturbance Index (*EDI*).

Appendix S5. Methods used to test usefulness of the weighted Ecological Disturbance Index (EDI_L).

Appendix S6. Details of the grass removal experiment used.

Appendix S7. *SSI* index construction and method employed to identify native tree species based on this index.

Table S1. *Land use characteristics of studied pasture fields in Marqués de Comillas, southern Mexico.*

Table S2. *Land use characteristics of studied cornfields in Marqués de Comillas, southern Mexico.*

Figure S1. Differentiation in species composition of second growth forests from abandoned cornfields and pastures in Marqués de Comillas, southern Mexico.

Figure S2. Relationships between structural attributes of regenerating forests and the Ecological Disturbance Index (EDI).

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