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.

Key words: agricultural land uses; dispersal limitation; establishment limitation; Mexico; tree demography; tropical rainforest; second-growth forests; secondary succession

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 & Pérez, 2006), the potential for forest regeneration in abandoned fields (Chazdon 2014), and the restoration of degraded lands (Holl 2012). Fragments

often are less than 100-ha and undergo ecosystem degradation due to edge effects and other threats (Benítez-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, 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, 2016). Therefore, understanding ecological legacies of agricultural land uses (Foster *et al*. 2003, Chazdon 2003), identifying land uses that promote forest regeneration, and developing ecological tools to restore degraded lands (Hobbs & Harris, 2001, Hobbs and Cramer 2007, Holl 2012) 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).

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 pinpointing ecological factors playing critical roles for dispersal and establishment of colonizing 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. Finally, in the third topic we integrate disturbance regimes caused by different agricultural land uses and the landscape composition to predict structural attributes (density, biomass, species diversity) of second-growth forests in

HMLs; also, in this section we provide guidelines for identifying native tree species that can help in restoration of degraded lands. We approach these issues mostly using studies we 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 rainforest 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, Martinez-Ramos *et al*. 1988). Deforestation and subsequent agricultural land uses, in contrast, generate disturbances of much larger size, severity and duration (Foster *el al*. 2003, Holl & Aide 2011, Laurence *et al.* 2014). Such anthropogenic disturbances are new events in the evolutionary history of rainforest 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 field size enlarges and distance to forest remnants (*i.e*. seed sources) increases. Also, dispersal limitation increases 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 of gray boxes in the sketch). At the same time, the biophysical environmental conditions depart from those enabling the survival, growth and or reproduction of most rainforest 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).

Regarding the above framework, in the following sections we analyze the demography of typical pioneer tree species to exemplify 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). 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 three years after the abandonment of a cornfield (see methods in Appendix 1, supporting information).

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 regenerative bottleneck. However, important differences in seed

121 biology among species suggest that an increase in the harshness of agricultural land use may
122 have different regenerative consequences for these species. Seeds of *Trema* and *Cecropia*
123 *obstusifolia* are small, copiously and continuously produced (Álvarez-Buylla & Martínez-Ramos
124 1990), and dispersed by a rich array of highly mobile vertebrates (Estrada *et al*. 1984). In
125 contrast, the larger seeds of *Trichospermum mexicanum* are wind-dispersed, and produced only
126 during the dry season (Ibarra-Manríquez *et al*. 1991). These reproductive differences partially
127 explain why the year around abundance of seeds was over one order of magnitude smaller in
128 *Trichospermum* than in the other two species. *Trichospermum* seeds were 30 times more
129 abundant in soil than in the seed rain, suggesting a long-lasting seed bank. In contrast, *Trema*'s
130 seed rain was far more abundant than soil seeds, suggesting these seeds do not accumulate in the
131 soil. In *Cecropia* seed rain and soil seed abundances were similar, also suggesting no seed
132 accumulation. In old-growth forest sites, *Cecropia* soil seeds have very short lifespans (less than
133 ten days), suffering high predation rates by insects and pathogens; they are dynamically replaced
134 by newly and abundant dispersed seeds (Álvarez-Buylla & Martínez-Ramos 1990). Also, in
135 recently abandoned cornfields (Corzo-Domínguez 2007) and pastures (García-Orth & Martínez-
136 Ramos 2008) *Cecropia* soil seeds suffered predation rates close to 100% within few days. While
137 *Trema* has similar seed population dynamics, *Trichospermum* may be much better in resisting
138 predation and diseases. In terms of our conceptual framework (Fig. 1), regeneration potential of
139 pioneer species like *Cecropia* and *Trema* would be more sensitive to extensive (*i.e.* large-sized)
140 agricultural land uses (*e.g*. cattle pastures or monocultures of several dozen hectares; Fig. 1),
141 which reduce animal seed dispersal, while species like *Trichospermum* could be more sensitive
142 to severe land uses (*i.e.* those causing high *in situ* environmental modification; Fig. 1) that reduce
143 or eliminate the soil seed bank.

144 Two years after field abandonment, *Cecropia* was the only species with seedlings (Fig.
145 2a) indicating strong establishment limitations for *Trema* and *Trichospermum*. Likely, as soon as
146 colonizing vegetation forms a closed canopy cover, and light availability declines in the
147 understory, seeds of these two pioneer trees were unable to germinate and/or newborn seedlings
148 died soon after emergence. *Trema* and *Trichospermum* were less shade-tolerant than *Cecropia*,
149 and probably prosper better in large open fields. For *Trema* this was confirmed in Barro
150 Colorado Island where this tree requires larger gaps than *Cecropia* to regenerate (Brokaw 1987).
151 *Trichospermum* could be intermediate as indicated by the fact that this species exhibited a middle
152 density of juvenile trees between *Trema* and *Cecropia* in our abandoned cornfields (Fig. 2). The
153 abundant seedlings and saplings of *Cecropia*, however, suffered high mortality rates (> 60% per
154 year) and only 2.3% of the juveniles-1 (50-150 cm height) reached sizes larger than 1 cm DBH
155 over the studied year (Fig. 2). In contrast, *Trichospermum* exhibited lower mortality and higher
156 progression rates in the juvenile stages, increasing its survival and growth as individuals transited
157 to further life cycle stages. *Trema* exhibited high mortality and low progression rates in juvenile
158 and pre-mature stages (4.1-8 cm DBH). These results are indicative of the strong competition
159 that pioneer trees endure during the first years of old-field succession (van Breugel *et al.* 2012),
160 and likely indicate differences in the ability of the species to use light resources and to cope with
161 natural enemies (herbivores and diseases) in juvenile and pre-mature stages. In the three species,
162 mortality decreased and growth increased markedly in the mature stage, when tree crowns get
163 exposed to direct sunlight.

164 As a net result of these demographic transitions and ecological filters, *Trichospermum*
165 recruited more mature trees than *Trema* and *Cecropia*, which reached mature sizes only three
166 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, van Breugel *et al*. 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 dynamical attributes of regenerating forests (Levy-Tacher *et al*. 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 *et al*. 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 (Table S1 and Table S2), but were located within the same geomorphology unit and landscape matrix (see Appendix 2 for methods; supporting information).

Six years after the abandonment of our studied fields, shrub and tree assemblages (height > 1 m) in the pastures were 2-15 times lower in stem density, basal area (a surrogate for above ground 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 cornfield conditions, 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 understorey (3 species covering 60% of basal area; Fig. S1a, supporting information). 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 (6 species covering 60%; Fig. S1a, supporting information). Additionally, 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

213 non-metric multidimensional scaling analysis fully separated cornfields from pastures along the
214 main ordination axis (Fig. S1b, supporting information). While typical pioneer trees colonizing
215 canopy gaps in old-growth forest (such as *Trichospermum*, *Ochroma*, *Helicarpus* and *Piper*)
216 dominated the cornfields, species related to savanna-like vegetation (*e.g. Byrsonima crassifolia*,
217 *Curatella americana* and *Vismia camparaguey*) dominated the pastures (Fig. S1a, supporting
218 information).

219 Similar legacies of agricultural land uses were found in a long-term study that contrasted
220 successional forest pathways between abandoned clear-cuts, which represented a relative mild
221 land use, and cattle pastures, which represented a harsh land use (including multi-episodes of
222 burning), in Manaus, Brazil (Mesquita *et al*. 2015). Twenty-five years after abandoned, diverse
223 and structurally complex second-growth forests developed in the clear-cuts while structurally
224 simple and low diverse ones developed in the pastures. Another example is in regenerating forest
225 near Tefé, Brazil, where swidden agriculture land use intensity also reduced regeneration and
226 impacted the regenerating community (Jakovac *et al*. 2015). These studies strongly support the
227 hypothesis that forest regeneration rate (gain in species diversity and biomass per unit of time
228 and space) is reduced with the harshness of the land use, especially when burning recurrence is
229 involved, and that contrasting agricultural land uses may lead to divergent successional
230 pathways.

231 ASSESSING REGENERATION EFFECTS IN AGRICULTURAL LAND USE GRADIENTS.- As different
232 agricultural land uses occur at the same time in HMLs, their joint impact on forest regeneration
233 potential needs to be assessed (*e.g.* Holl 2007, Pascarella *et al.* 2000). To predict forest
234 regeneration potential in any abandoned agricultural field in a complex multi-land use HML we
235 constructed a simple index based on information provided by landowners and farmers (Zermeño-

236 Hernández *et al*. 2015). Our Ecological Disturbance Index (*EDI*) was derived from the analysis
237 of agricultural land uses as ecological disturbance regimes (*sensu* Picket *et a*l. 1985). *EDI*
238 incorporates, in an additive way, three major disturbance components: size (field area in
239 hectares), duration (years of agricultural use) and severity (including fire incidence, chemical
240 use, machinery use, stocking rate, and tree cover in the field; see Appendix 3, supporting
241 information). The index varies from 0 (no disturbance) to 3 (maximum disturbance; Zermeño-
242 Hernández *et al.* 2015).

243 We tested EDI's usefulness to predict forest regeneration potential in an experiment in
244 Marqués de Comillas (see Appendix 4, supporting information), where forest regeneration was
245 monitored in recently abandoned fields differing widely in *EDI* values. Plant density, species
246 density, and above ground biomass of shrubs, trees and lianas (10-150 cm height) were
247 quantified at the time of field abandonment and two years later, in permanent plots near (< 5 m)
248 and far (> 100 m) from nearest forest remnants. Regeneration rates in abundance, species density
249 and species diversity decayed exponentially with *EDI* (Zermeño-Hernández *et al*. 2015). In
250 contrast, physiochemical soil variables measured at the time of abandonment (for details see
251 Zermeño-Hernández *et al.* 2015) failed to explain the among field variation in regeneration rates.
252 Only microclimate variables such as air temperature, relative humidity, and vapor pressure
253 deficit predicted regeneration rates. To our surprise, the farmer-based simple and cheap-to-get
254 *EDI* index indicated the recovery of abundance, species density and diversity as well as
255 measurements of microclimate conditions, which are costly (*e.g*., equipment requirement) and
256 time consuming, especially when rapid assessment of many agricultural fields is required.

257 Dispersal limitation plays an important role in forest regeneration potential (Reid *et al*.
258 2015). Plant density and diversity decreased significantly with *EDI* only near edges of forest

remnants (Fig. S2, supporting information), implying that severe and long-lasting agricultural land use strongly limits forest regeneration even under abundant seed rain (I. Zermeño-Hernández pers. obser.). In contrast, the lack of EDI impact far from forest edges (Fig. S2, supporting information) 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 two-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 & Picket 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

282 imposed by the different agricultural land uses (affecting *in situ* propagule availability and
283 environmental conditions in the abandoned fields). However, the cumulative impact of
284 disturbance, caused by different land uses occurring in a landscape, on the ecological properties
285 of second-growth forest still needs to be assessed (Chazdon 2014).

286 We developed the *EDI*-based Ecological Disturbance Landscape Index (EDI_L, Zermeño-
287 Hernández *et al*. 2016) for this purpose and tested the hypothesis that structural attributes (stem
288 density, species density, species diversity, and biomass) of second-growth forests are reduced
289 with increasing disturbance regimes, associated with the mosaic of land uses in the landscape.
290 EDI_L is calculated as $EDI_L = \Sigma\ EDI_i * p_i$, where EDI_i is the average *EDI* value for all fields with
291 land use type i, and p_i is the cover proportion of that land use type in the landscape. We tested
292 the usefulness of this index in a study in Marqués de Comillas. To quantify EDI_i for different
293 agricultural land uses, Zermeño-Hernández *et al*. (2016) did semi-structured interviews with 68
294 owners of 156 agricultural fields encompassing 13 different agricultural land uses. The EDI_i
295 values ranged from 0.60 to 0.75 for agroforestry systems (*e.g*. coffee, orchard, cocoa plantations)
296 from 1.3 to 1.5 to 1.9 monocultures (*e.g*. cornfields, bean and rice fields) and was 1.9 for
297 extensive farming (*e.g*. pastures, oil palm plantations). We incorporated in EDI_L the proportion
298 of area occupied by the old-growth forest remnants, assigning it the value of $EDI = 0$, and of
299 patches of secondary vegetation, assigning a value of $EDI = 0.25$, considering that old-growth
300 forest represent the undisturbed condition and that secondary forests may attain important levels
301 of biodiversity and biomass, as documented for other studies conducted in Marqués de Comillas
302 (van Breugel *et al.* 2006, 2007; Lohbeck *et al*. 2014, 2016) and in other Neotropical regions
303 (Norden *et al.* 2015, Poorter *et al*. 2015, 2016). This value, however, is tentative because *EDI* of
304 secondary forests may change from a relatively high starting value, defined by the disturbance

305 regime imposed by the agricultural land-use before abandonment (Mesquita *et al*., 2015;
306 Zermeño-Hernández *et al*., 2015) to a value of 0, if the secondary forest, over time, reaches a
307 structure and function similar to that of the old-growth forest.

308 Our study system consisted of ten landscapes (1-km^2 each) for which EDI_L values, as
309 well as different structural community attributes and fallow age (years) of second-growth forests,
310 were quantified (see Appendix 5, supporting information). Overall, tree density did not change
311 with EDI_L but species density ($R^2 = 0.58$, $P < 0.01$), basal area ($R^2 = 0.92$, $P < 0.01$), and species
312 diversity (Inverse Simpson index, $R^2 = 0.45$, $P = 0.03$), decreased with EDI_L (Zermeño-
313 Hernández *et al*. 2016). Because these tree community attributes tend to increase with second-
314 growth forest age (Norden *et al*. 2015), and landscapes with low EDI_L values (*i.e*. recently
315 opened to agriculture) could have younger forests than landscape with high EDI_L values, we
316 checked that EDI_L effects were independent of forest age. For this, we obtained the mean fallow
317 age of secondary forests recorded in each landscape. Indeed, across landscapes mean structural
318 attribute values of secondary forests varied independently of mean fallow age (regression
319 analysis, $N = 9$, $P > 0.10$).

320 In our studied landscapes, EDI_L was largely determined by the percentage of land
321 covered by cattle pastures (%CP), which had the higher *EDI* value (Zermeño-Hernández *et al*.
322 2016). Pastures covered between 7 and 93% of the studied landscapes, and represented between
323 71 and 100% of the land covered by agriculture. Therefore, we expected that %CP in the
324 landscape could be a simpler indicator of the second-growth forest attributes. Indeed, species
325 density, species diversity, and basal area declined with %CP across landscapes (Fig. 3a-c). We
326 also expected that the values of the regenerating forest attributes would increase with the
327 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 (Fig. 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 Geographic Information Systems) 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: i) ecological quality (density, species diversity, biomass) of second-growth forests systematically decreases with increasing area of land uses inflicting high disturbance regimes (*e.g*. extensive cattle pastures) in the landscape, and ii) 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 agricultural land uses that inflict low disturbance regimes imbedded 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 knowing 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. 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% removal in only eight days (mostly by ants), and those of the late-successional trees *Brosimum alicastrum* (Moraceae) and *Dialium guyanense* (Leguminosae) suffered 80-100% 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%, and increased seedling emergence in 7% to 35% (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

374 seedlings (Holl *et al*. 2000, Hooper *et al*. 2005, Celis & Shibu, 2011). Grass removal enhanced
375 survival and growth of seedlings, fostering forest regeneration (Holl *et al*. 2000, Meli *et al*.
376 2015), under the condition of sufficient regenerative propagule availability. A grass removal
377 experiment we conducted in Marqués de Comillas exemplifies the combined effects of dispersal
378 limitation (*i.e.* distance to nearest forest fragment) and grass vegetation (*i.e.* establishment
379 limitation) as forest regeneration barriers. In two pastures close (< 500 m) and two pastures far
380 (> 1000 m) from nearest forest remnants, grass removal effects were assessed 3.5 years after
381 abandonment considering plant density, species density, and basal area of regenerating forests
382 (shrubs and trees ≥ 1 m height; see Appendix 6, supporting information). Forest attribute values
383 of all woody plants together were significantly higher in plots close to forest remnants than far
384 away, and grass removal increased only basal area in the close plots (Table 2). Only trees,
385 however, responded in all attributes both to distance and grass removal; close to forest remnants,
386 where trees were dominant, grass removal significantly increased all forest attributes, but far
387 away in shrub-dominated plots, grass removal had no effect on trees (Table 2). These results
388 support the view that forest regeneration is especially affected by dispersal limitation and that
389 elimination of the grass barrier can improve forest recovery, if seed sources are close (Holl *et al*.
390 2000, Benítez-Malvido *et al*. 2001, Hooper *et al*. 2005).

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

We developed a Species Selection Index (*SSI*; Martínez-Ramos & García-Orth 2007, Fuentealba *et al*. 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 7 (supporting information), *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 presence or absence of the fern cover (see methods in Appendix 7); in total, we tested six species. Eight months after transplantation only *Ochroma pyramidale* seedlings had higher survival in presence than in absence of the ferns (Fig. 4a). Height growth rate was higher in absence of the fern in five species, but *Ochroma* grew faster in presence of the 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 presence of the bracken fern. For now, we noted that species having *SSI* < 1 had leaf area gains in presence of the fern while species with

420 *SSI* > 1 had leaf area losses (data not shown). This suggests that species having high morpho-
421 physiological plasticity could perform well for restoring degraded fields as shown in other
422 studies (Martínez-Garza *et al.* 2005, 2013).
423 Of course, even species that require high economic investment for improving their
424 performance in the degraded site can be selected to recover desirable ecosystem functions and
425 services and to increase species and functional diversity of the restoring vegetation. A limitation
426 of *SSI* is that pilot studies are needed to assess seedling performance with and without care,
427 requiring additional and sometimes high resource investment. The *SSI* index can be improved by
428 considering the net present and future value of transplanting seedlings. For example, as time
429 passes the initial investment decreases (depending, among other things, on inflation rates) while
430 future value can increase if the transplanted species offer valuable uses (*e.g*. fruits, timber, fire-
431 wood, fodder for cattle). The incorporation of societal criteria for selecting native tree species for
432 restoration would also increase the usefulness of the *SSI* index (Meli *et al*. 2014).
433
434 **CONCLUDING REMARKS**
435
436 This review shows important guidelines for maintaining forest regeneration potential in HMLs.
437 First, at the field (local) scale, this potential is enhanced as the size, duration and disturbance
438 severity of the agricultural land use decline and the regeneration bottlenecks become weaker.
439 Agricultural land uses maintaining high levels of tree cover, minimizing the use of fire,
440 agrochemicals, and heavy machinery, and having short-use periods, allow forest regeneration
441 best. Diverse agroforestry and agro-ecological systems (Schroth *et al*. 2004, Bhagwat *et al.* 2008,
442 Perfecto & Vandermeer 2008), and those preserving remnant trees of native species, which

443 function as regeneration nuclei (Guevara *et al*. 1986, Harvey & Haber 1998, Schlawin & Zahawi
444 2008, Derroire *et al*. 2016), represent examples of such land uses. Second, at the landscape scale,
445 the ecological quality (*e.g*. high species diversity and biomass) of regenerating forest increases
446 with the extent of old-growth forest remaining in the landscape, which function as major source
447 of species in the regeneration process at the field scale. A promising composition of HMLs
448 where agricultural production and biodiversity conservation can be conciliated is a mosaic of
449 agroforestry and agro-ecological systems imbedded in a matrix of old-growth and second-growth
450 forests. Agricultural fields must retain forest cover in their vicinity (*e.g*., live fences and other
451 living structures acting as biological corridors) to facilitate the movement of pollinators, seed
452 dispersers, herbivores, and other animals playing key roles in forest regeneration. The area
453 devoted to second-growth forests would be retained for long time periods, as biodiversity and
454 ecosystem functions and services of these forests increase with forest age (Chazdon 2014);
455 enriching secondary forests with species providing valuable timber and non timber forests
456 products, and developing sustainable and economically viable forest management programs for
457 landowners, could help to reach this objective (Lamb *et al*. 2005, Chazdon *et al*. 2009). Ideally
458 forest regeneration would be promoted at the boundaries of old-growth forest fragments,
459 especially the small ones, to buffer edge effects and promote forest connectivity across the
460 landscape. Conserving high levels of forest cover in HMLs also promotes preservation of native
461 fauna, including large vertebrates (*e.g*. Banks-Leite *et al*. 2014, Muench & Martínez-Ramos
462 2016) that play important ecological roles (as pollinators, seed dispersers, controllers/regulators
463 of diseases, among other functions) in forest regeneration and maintenance of biodiversity in the
464 landscape (Dirzo *et al*. 2014).

465 Presently, in most HMLs just one or few extensive agricultural land uses (*e.g*. large
466 pastures, conventional soy fields, commercial tree/pam plantations), often promoted by
467 governmental or private incentives, tend to dominate. It is an extraordinary challenge to change
468 this monodominant land use trend into the diverse mosaic described above, as this depends on a
469 complex suite of societal and ecological factors. Modifying present agricultural practices is
470 critical for encouraging socially and environmentally accepted sustainable systems (Castillo &
471 Toledo 2000, Perfecto & Vandermeer 2008). Future dynamical landscape studies would adopt
472 socio-ecological, transdisciplinary, approaches with the participation of key stakeholders, to look
473 for alternative landscape managing strategies (*e.g*. land sharing *vs*. land sparing; Phalan 2011),
474 and assessing the feasibility of transforming the landscape into a diverse mosaic in which
475 biodiversity and human livelihoods can be balanced.
476
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753 TABLE 1. Mean (± SE) values of structural attributes of regenerating forests six years after
754 the abandonment of cornfields (N = 3) and cattle pastures (N = 2) in Marques de Comillas,
755 Southeastern Mexico. For each attribute, land uses not sharing same letter are significantly
756 different (P < 0.05, Generalized Liner Models).
757

	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]

758

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 m², species density in species/750 m², and basal area in m²/750 m²; 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]

LEGENDS FOR FIGURES

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).

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

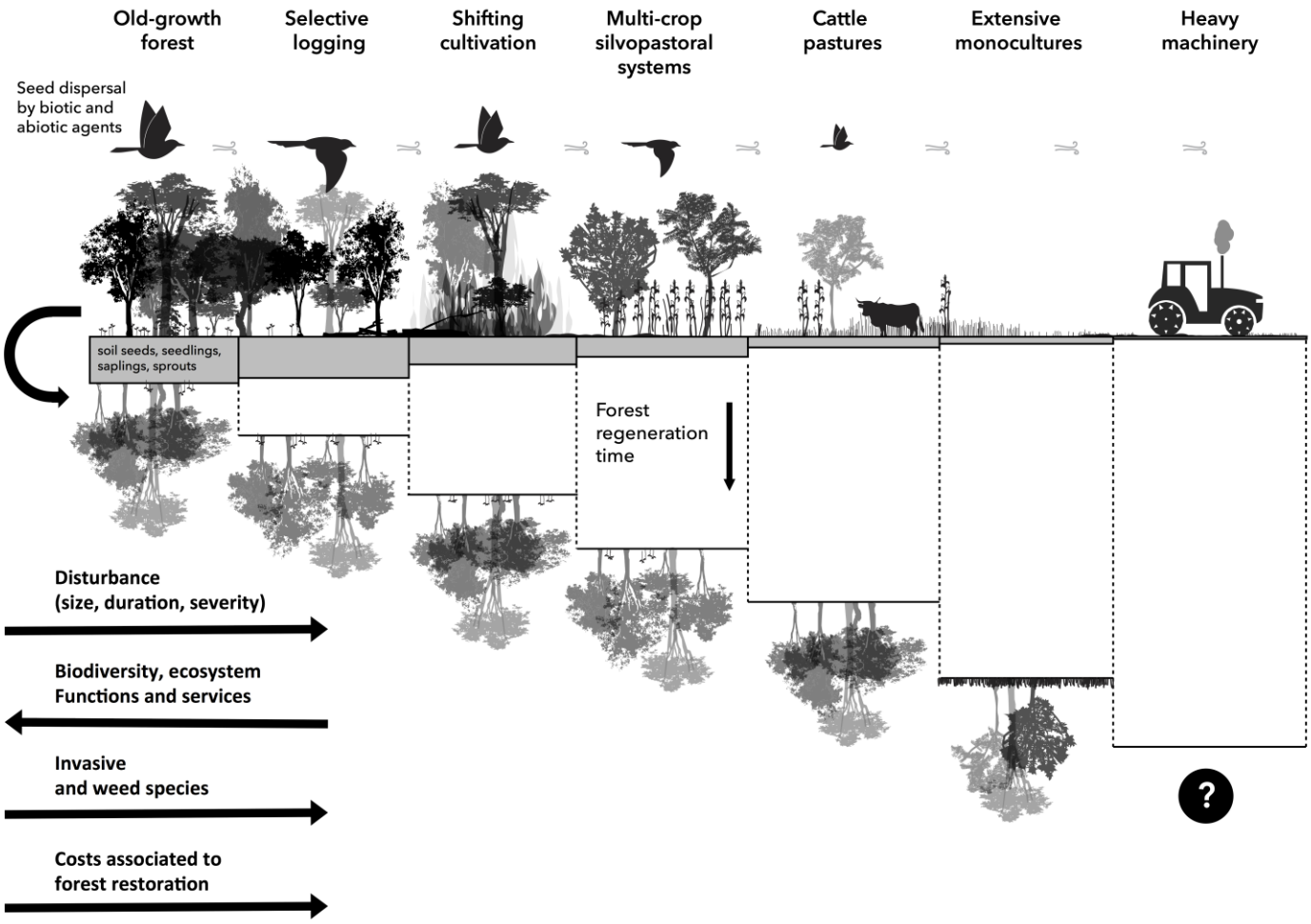
II (151 cm tall to 2.5 cm DBH), Juveniles III (2.6 to 5 cm DBH), Pre-matures (5.1 to 10 cm DBH) and Matures (> 10 cm DBH). In these categories, for a time period of one year, right-headed horizontal arrows represent progression from one to the next stage, left-headed horizontal arrows represent reduction 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.

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 x 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.

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 eight months after transplantation under the presence (+BF) and removal of the above ground fern

tissues (-BF); the removal of such tissues was repeated every two months to control fern regrowth. (b) Absolute growth rate of seedlings after eight 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 six months after transplantation; arrows indicate the species more recommendable for restoration of pastures covered by bracken fern in the study site.

FIGURE 1


Old-growth forest
Selective logging
Shifting cultivation
Multi-crop silvopastoral systems
Cattle pastures
Extensive monocultures
Heavy machinery
Seed dispersal by biotic and abiotic agents
soil seeds, seedlings, saplings, sprouts
Forest regeneration time
Disturbance (size, duration, severity)
Biodiversity, ecosystem Functions and services
Invasive and weed species
Costs associated to forest restoration
?

822 FIGURE 2

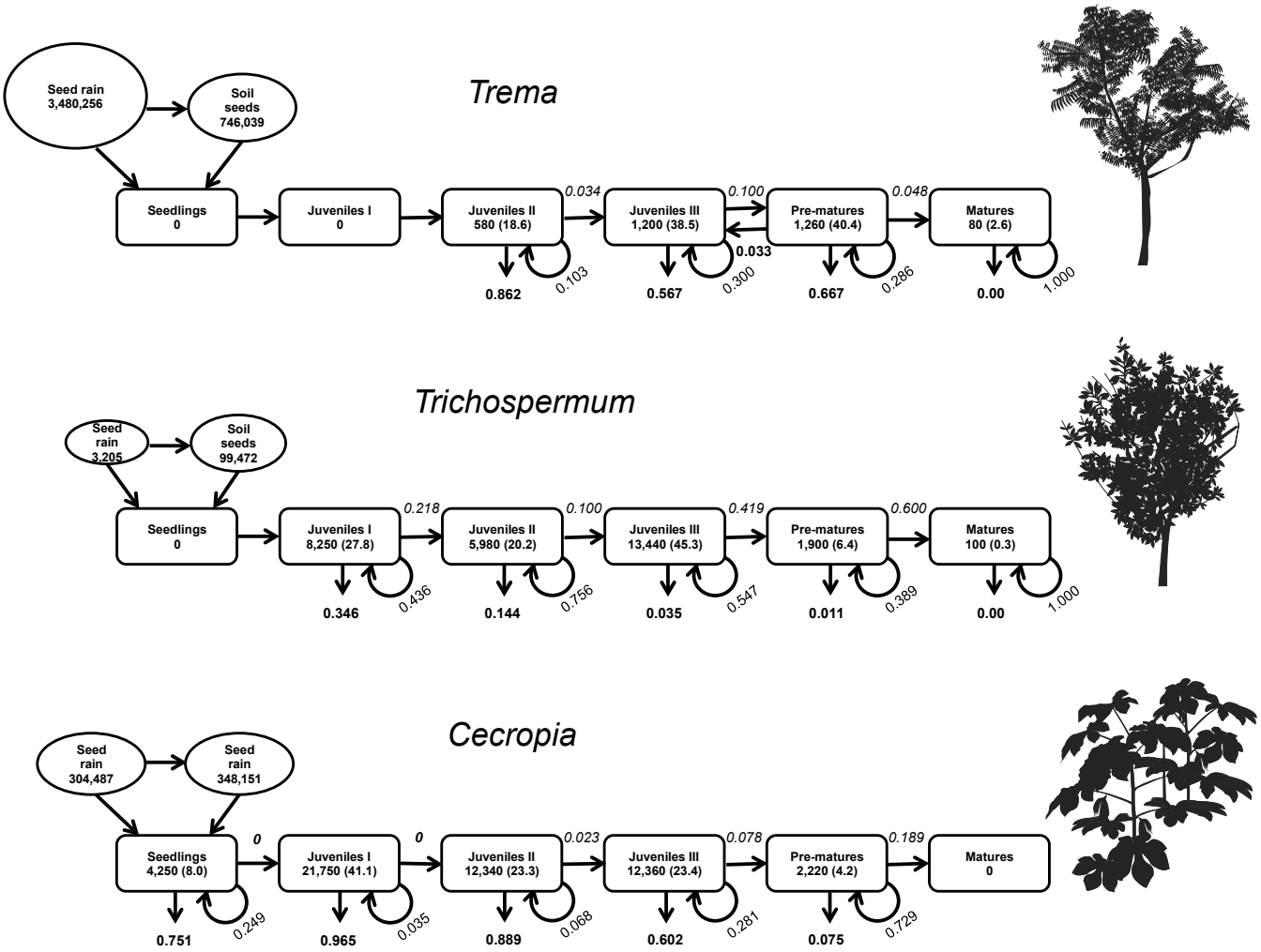
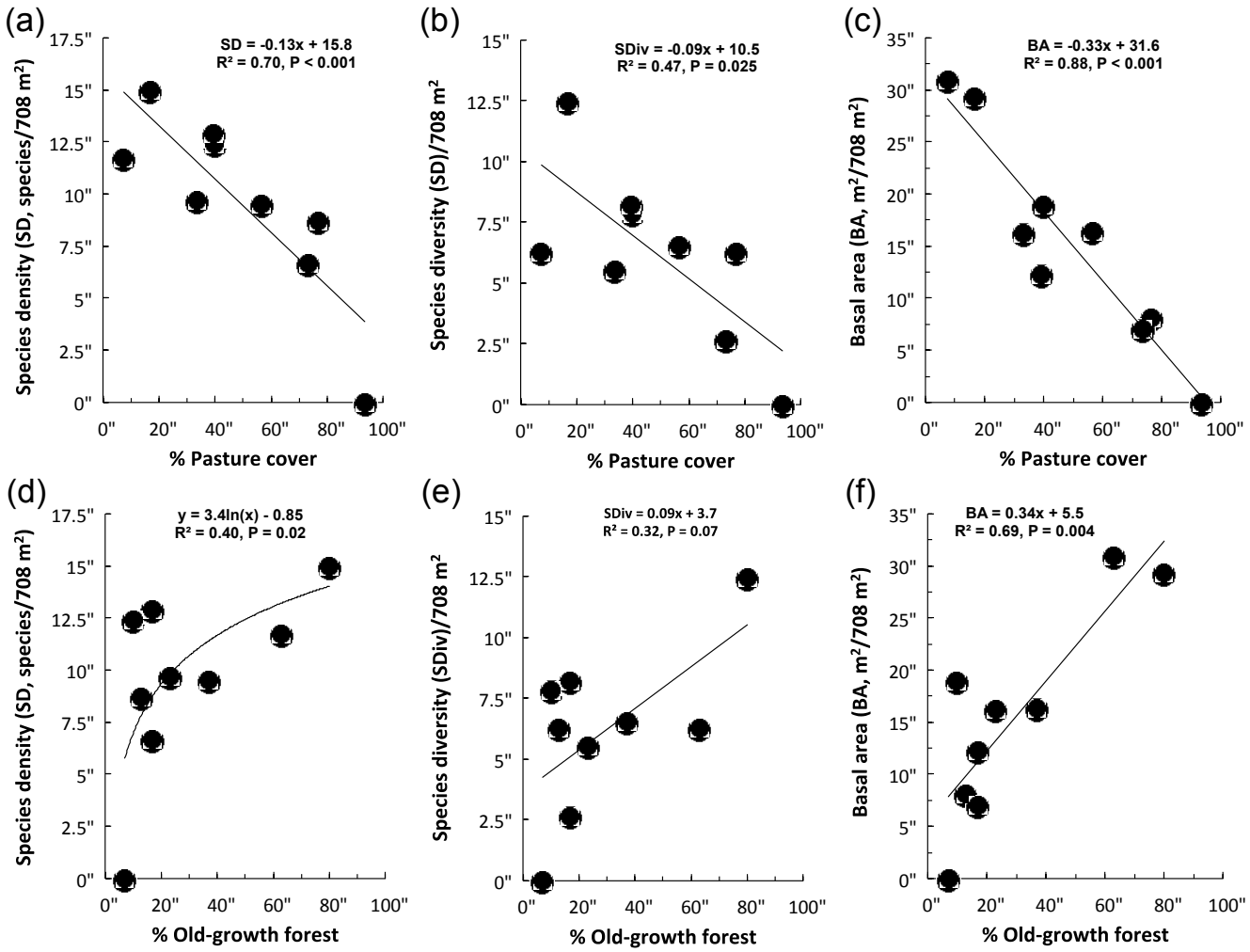
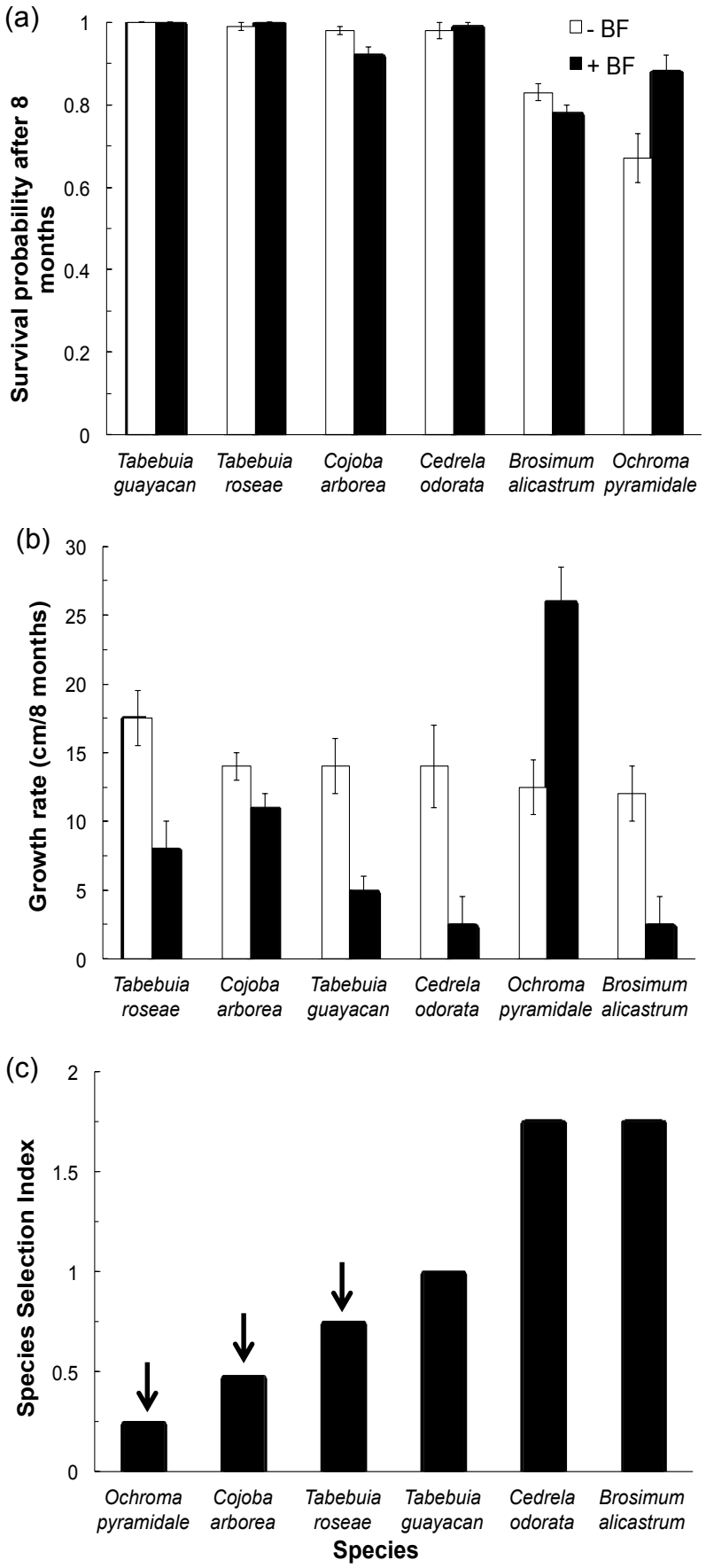

Trema
Seed rain 3,480,256
Soil seeds 746,039
Seedlings 0
Juveniles I 0
Juveniles II 580 (18.6)
Juveniles III 1,200 (38.5)
Pre-matures 1,260 (40.4)
Matures 80 (2.6)
0.034
0.100
0.048
0.033
0.862
0.103
0.567
0.300
0.667
0.286
0.00
1.000
Trichospermum
Seed rain 3,205
Soil seeds 99,472
Seedlings 0
Juveniles I 8,250 (27.8)
Juveniles II 5,980 (20.2)
Juveniles III 13,440 (45.3)
Pre-matures 1,900 (6.4)
Matures 100 (0.3)
0.218
0.100
0.419
0.600
0.346
0.436
0.144
0.756
0.035
0.547
0.011
0.389
0.00
1.000
Cecropia
Seed rain 304,487
Seed rain 348,151
Seedlings 4,250 (8.0)
Juveniles I 21,750 (41.1)
Juveniles II 12,340 (23.3)
Juveniles III 12,360 (23.4)
Pre-matures 2,220 (4.2)
Matures 0
0
0
0.023
0.078
0.189
0.751
0.249
0.965
0.035
0.889
0.068
0.602
0.281
0.075
0.729

FIGURE 3


(a)
SD = -0.13x + 15.8
R² = 0.70, P < 0.001
Species density (SD, species/708 m²)
% Pasture cover
(b)
SDiv = -0.09x + 10.5
R² = 0.47, P = 0.025
Species diversity (SD)/708 m²
% Pasture cover
(c)
BA = -0.33x + 31.6
R² = 0.88, P < 0.001
Basal area (BA, m²/708 m²)
% Pasture cover
(d)
y = 3.4ln(x) - 0.85
R² = 0.40, P = 0.02
Species density (SD, species/708 m²)
% Old-growth forest
(e)
SDiv = 0.09x + 3.7
R² = 0.32, P = 0.07
Species diversity (SDiv)/708 m²
% Old-growth forest
(f)
BA = 0.34x + 5.5
R² = 0.69, P = 0.004
Basal area (BA, m²/708 m²)
% Old-growth forest

825 FIGURE 4


(a)
Survival probability after 8 months
1
0.8
0.6
0.4
0.2
0
- BF
+ BF
Tabebuia guayacan
Tabebuia roseae
Cojoba arborea
Cedrela odorata
Brosimum alicastrum
Ochroma pyramidale
(b)
Growth rate (cm/8 months)
30
25
20
15
10
5
0
Tabebuia roseae
Cojoba arborea
Tabebuia guayacan
Cedrela odorata
Ochroma pyramidale
Brosimum alicastrum
(c)
Species Selection Index
2
1.5
1
0.5
0
Ochroma pyramidale
Cojoba arborea
Tabebuia roseae
Tabebuia guayacan
Cedrela odorata
Brosimum alicastrum
Species