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The soil seed bank in abandoned tropical pastures: source of regeneration or invasion?

El banco de semillas en pastizales tropicales abandonados: fuente de regeneración o de invasión?

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Abstract. We assessed the availability of both pioneer and non-native species in the soil seed bank of old-growth forest and recently abandoned pasture, to evaluate whether the soil seed bank in these pastures represents a source of regeneration of species from adjacent old-growth forest or of invasion by non-native species. Our study was conducted at Selva Lacandona, Chiapas, Mexico. Soil samples were randomly collected from 6 sites in old-growth forest, and 6 sites in abandoned pastures. Seedlings from soil samples were identified and classified into pioneer, non-native (weeds/graminoids), and other forest species. Pioneer species seeds were virtually absent in pastures, but represented ~30% of seeds in the forest. Non-native species comprised ~99% of the soil seed bank in pastures. In the forest, soil seed bank density of weeds and graminoids decreased with increasing distance (up to 4 km) from agricultural fields, and comprised up to 25% (Mean \pm 1SE= 16 ± 7) of the seed bank. Our results show a near total elimination of pioneer species from the soil seed bank in pastures, and considerable invasion of the borders of the Montes Azules reserve by seeds of non-native species. Thus, in the region studied, the soil seed bank in abandoned pastures represents a source of invasion by non-native species into old-growth forest rather than a potential source of forest regeneration.

Key words: *Cecropia*, tropical rain forest, Selva Lacandona, Chiapas, pioneer regeneration, weed invasion.

Resumen. Para evaluar si el banco de semillas en pastizales abandonados representa una fuente de regeneración o de invasión por especies no-nativas para el bosque maduro se evaluó la presencia de especies pioneras y no-nativas en el banco de semillas de bosque maduro y pastizales recién abandonados en la selva lacandona, Chiapas, México. Se recolectaron muestras de suelo en 6 sitios de bosque maduro y de pastizales abandonados. Las semillas germinadas fueron identificadas y clasificadas en especies pioneras, no-nativas (malezas/graminoides) y otras especies de bosque. Las especies pioneras estuvieron virtualmente ausentes en los pastizales, pero representan ~30% de los registros en bosque maduro. Las especies no-nativas representan ~99% del banco de semillas en los pastizales. En el bosque maduro, el banco de semillas de malezas/graminoides decrece con el incremento de la distancia de campos agrícolas y representa hasta el 22% del banco de semillas. Nuestros resultados muestran una importante supresión de las especies pioneras en el banco de semillas de los pastizales y una considerable invasión de los bordes de la Reserva Montes Azules por semillas de especies no-nativas. En la región de estudio, el banco de semillas en pastizales abandonados representa una fuente de invasión por especies no-nativas para el bosque maduro más que una fuente potencial de regeneración.

Palabras clave: *Cecropia*, bosque tropical lluvioso, selva lacandona, Chiapas, regeneración de especies pioneras, invasión de malezas.

Introduction

Tropical rain forests are being continuously cleared and converted to pasture at high rates for cattle (Hecht, 1993; Nepstad et al., 1996; Florentine and Westbrooke, 2004). This anthropogenic disturbance has profound environmental

and ecological effects, which include alteration of the gas composition of the atmosphere, loss of biodiversity and ecosystem functions and services (Chazdon et al., 2009), and threatening of forest regeneration potential (Gómez-Pompa et al., 1972; Esquivel et al., 2008). In addition, abundant weed populations often become established in these pastures (Kohli et al., 2006; Vieira and Proctor, 2007) which can then become infection foci of invasive species for the remnants of nearby old-growth forest.

The soil seed bank of pioneer species plays an

important role in post-disturbance regeneration and secondary succession of tropical rain forest (Garwood, 1989; Bazzaz, 1991; Aide and Cavelier 1994). Any factor which depletes the soil seed bank of pioneer species could therefore diminish forest regeneration potential (Wijdeven and Kuzee, 2000; Vieira and Proctor, 2007). For example, the commonly used slash-and-burn practice of pasture preparation and maintenance can reduce seed availability by eliminating mature pioneer plants. As a result of this loss, most seeds of pioneer species in pastures must arrive from external sources, and through various dispersal agents (Guevara and Laborde, 1993; Holl, 1998; Medellín and Gaona, 1999). However, most seeds dispersed in this manner fall at distances of less than a few dozen metres from nearby forest remnants (Aide and Cavelier, 1994; Martínez-Garza and González-Montagut, 1999; Cubiña and Aide, 2001). Subsequent predation by insects (mostly ants) and small mammals (e.g. mice) can further reduce the abundance of pioneer species seeds in pasture (Nepstad et al., 1996; Wijdeven and Kuzee, 2000; Cubiña and Aide, 2001; García-Orth and Martínez-Ramos, 2008). It has been suggested that pioneer soil seed bank density declines with intensity of land use and with increasing size of pasture (Wijdeven and Kuzee, 2000; Esquivel et al., 2008). However, few studies have estimated the reduction of pioneer species in the soil seed bank of pastures, relative to that of nearby old-growth forest (Aide and Cavelier, 1994; Wijdeven and Kuzee, 2000).

Productivity of tropical pastures, especially those in nutrient-poor sites, tends to undergo a rapid decline (Buschbacher et al., 1988; Asner et al., 2004). This is associated with the proliferation of weed species that are capable of dominating the seed bank in abandoned pastures (Nepstad et al., 1996; Wijdeven and Kuzee, 2000; Vieira and Proctor, 2007). Due to the fact that the seeds of these species are capable of wide dispersal, abandoned pastures may become a source of invasive species for nearby old-growth forest remnants. However, these species are in general heliophiles and their invasiveness in the forest depends on disturbances, such as canopy gaps, forest fragmentation, etc (Kohli et al., 2006). This biological invasion may produce important negative ecological effects within the forest, as invasive species can threaten native biodiversity and alter the structure and function of the whole ecosystem (Asner et al., 2004; Kohli et al., 2006).

While several studies have evaluated the structure and composition of soil seed banks in the tropics, few have documented the influence of pastures on the relative availability of pioneer and non-native species within the seed bank (Florentine and Westbrooke, 2004). An understanding of this process is critical to the

identification of appropriate pasture management regimes which promote forest regeneration and prevent the proliferation of weeds or graminoids. This is an issue of great importance, considering the continued expansion of human-transformed landscapes in the tropics (Harvey et al., 2008; Chazdon et al., 2009).

In this paper, we studied soil seed bank structure and composition in old-growth forest and pasture sites in the Selva Lacandona region, at the border between the Montes Azules Reserve and the Marqués de Comillas region. The former is a MAB-UNESCO reserve, while the latter is an extensive agricultural area in southeast Mexico. Specifically, we assessed the availability of pioneer and non-native species (weeds and graminoids) in the soil seed banks of old-growth forest and recently abandoned pastures in order to evaluate whether the pasture soil seed bank represents a source of regeneration or a source of invasion by non native plants in old-growth forest. Our specific objectives were (1) to assess the availability of seeds of pioneer and non-native species (weeds and graminoids) in soils of recently abandoned pastures, (2) to assess the extent of invasion of old-growth forests by seeds of non-native species, and (3) to explore whether the density of seeds of non-native species in old-growth forest is related to distance from the nearest agricultural fields. Finally, we directly compared our results with those of previously published studies in the Neotropics.

Materials and methods

Study site. The study was carried out in the south of the Selva Lacandona region, at the border between the Montes Azules Biosphere Reserve (MAB-UNESCO) and Marqués de Comillas Region (MCR), in the southern state of Chiapas, Mexico (16°01' N, 90°55' W, Fig. 1). The Montes Azules Biosphere Reserve (MABR) covers approximately 331 000 ha and represents the largest area of protected rain-forest in Mexico. The elevation ranges between 100 and 300 m asl, and the climate is warm and humid, with an average annual precipitation of about 3 000 mm and a mean annual temperature of about 25 °C (INE, 2000). The dominant vegetation in this area is tropical rain forest (*sensu* Richards, 1996). Previous studies have identified different geomorphologic units in the area, in which forest structure, diversity and composition vary in line with changes in soil and topography (Siebe et al., 1996; Ibarra-Manríquez and Martínez-Ramos, 2002). In this study, we controlled this environmental variation by utilizing those areas composed exclusively of low-lying hills. This unit is well defined, with sandy or limestone

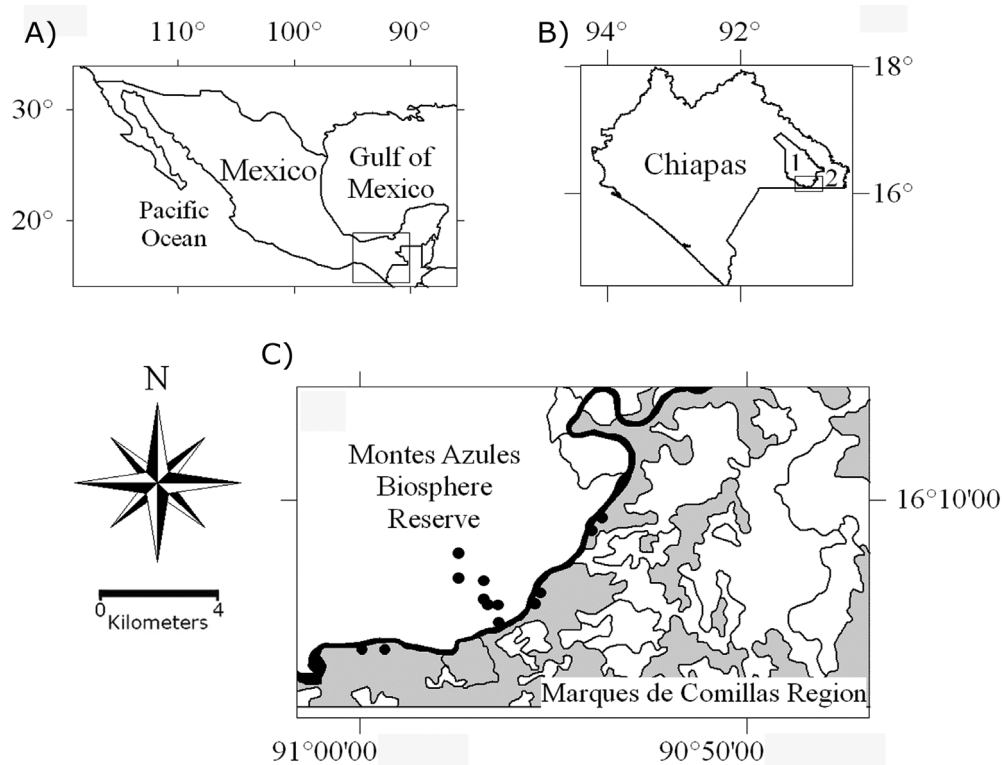


Figure 1. Location of the study site. In A) the state of Chiapas in Southeast Mexico is shown. In B) the polygon of Montes Azules Biosphere Reserve (MABR=1) and the Marqués de Comillas Region (MCR=2) at the East of Chiapas are shown. The rectangle in B) is amplified in C), and shows the MABR separated from the MCR by the Lacantun River and the study sites: closed squares within the MABR represent the old-growth forest and closed circles in the MCR represent pasture sites. The star indicates the location of the Chajul Field Station. In the MABR, the tropical rain forest dominates (white areas). By contrast agricultural and pasture lands (gray) dominate the edge of the border of MCR, although important old-growth forest remnants are also found (IG-UNAM 2002).

soils which are low in both nutrients and available water (Siebe *et al.* 1996). *Dialium guianense* (Fabaceae); *Guarea glabra* (Meliaceae); *Ampelocera hottlei* (Ulmaceae) and *Spondias radlkoferi* (Anacardiaceae) are among the dominant canopy species (Ibarra-Manríquez and Martínez-Ramos, 2002; López-Toledo *et al.*, 2008). Low-lying hills form the largest geomorphologic unit in the area and it is among these that most pastures are established within the MCR.

The Marqués de Comillas Region (MCR), which is approximately 200 000 ha in area, is located to the east of the Lacantún River, and directly opposite one of the core zones of the Montes Azules Biosphere Reserve (Fig. 1). Human colonization started around 1970 and currently the MCR comprises a mosaic of old-growth rain forest (< 35%), secondary forest (16%), pasture (43%), and areas of other agricultural land-use (7%) (Zermeño, 2008). Pasture management includes the use of fire, low levels of agrochemicals, and non-mechanized techniques. High-

yielding non-native grass species are used to establish the pastures, although some of the pastures still contain remnant trees (García-Orth and Martínez-Ramos, 2010). On average, cattle density is approximately 3 head ha⁻¹ and cattle are rotated between pastures every month. The pastures are used for about 13 yr, at which point they are abandoned (Zermeño, 2008). The intensity of pasture management regime corresponds to the “moderate” category on the scale proposed by Uhl *et al.* (1988).

Sampling design. Our study consisted of 6 pasture and 6 old-growth forest sites. The forest sites were located within the MABR, at distances between 1.5 and 4 km from the Lacantun River edge, which represent the border of the reserve and the agricultural fields, in the area under the supervision of the Chajul Field Station (Fig. 1). Using a geo-referenced map, we measured distance to agricultural areas as the shortest distance between each old growth forest study site and the nearest bank of the Lacantún River, considering that pasture and

agricultural lands occupied the whole length of the bank on the Marqués de Comillas side. In the MCR, 6 pastures with similar characteristics were selected (Appendix 1). Pasture size range was between 1 and 2 ha. Among the chosen pastures, distance from nearby forest remnants (degree of isolation) varied between 31 and 248 m, and length of time in use between 9 and 15 yr. Cattle stocking density was between 1 and 7 ha⁻¹, with a cattle rotation period of between 10 and 30 days, while the frequency of fires within the preceding 8 yr period varied between 1 and 4 (Appendix 1). The minimum distance between any old-growth forest and pasture site was 1 km.

Soil seed bank samples. At the beginning of August 1998 (the main rain-forest fruiting season in the study area; Martínez-Ramos, unpubl. data), 3 10 × 10 m plots, within a radius of 20 m, were randomly selected in each pasture and old-growth forest site. In each plot, 5 soil core samples were taken at random points with an auger (5 cm diameter × 10 cm depth). Sampling was completed within 1 week to avoid differences between habitats, and thus any temporal bias in seed availability and composition. To record viable seeds, the seedling emergence method was used (Ter Heerdt et al., 1999). Each soil core was divided into 2 layers: upper (0–5 cm depth) and lower (5–10 cm depth). Samples from each site were mixed in order to have 6 true replicates per layer in each of the 2 studied habitats. Each mixed sample was homogenized and placed in individual 20 × 30 × 0.5 cm trays (following Dalling et al., 1995). To prevent possible contamination of the soils with non-experimental seeds, trays were placed in a shade house established in an open site (> 80% full sun light) and covered by a layer of white plastic mesh (< 0.5 mm aperture) and transparent nylon sheet. The shade house was located in an open area of the Chajul Field Station, located outside the forest. To check for contamination, 10 additional control trays with sterilized substrate (by adding boiling water to soil samples) were included and allocated randomly among the experimental trays. The soil in each tray was watered to saturation every day in order to induce germination.

Seedling emergence was recorded every day for 80 days. A longer time period was originally planned, but measurement was interrupted by the onset of Hurricane Mitch (4th November 1998) which impacted the study area and produced unusual flooding at the edges of the Lacantún River where the shade house was located. Although an asymptotic trend in the germination rate was observed for both habitats, we cannot discount the possibility that seedling emergence may have continued had the flooding not halted the recording of emergence.

No seedling emergence was recorded in the control trays during the study period. Once recorded, all emerged

seedlings were carefully removed to avoid confusion with newly emerged plants. Samples of all morphospecies were grown in pots to facilitate taxonomic identification which was carried out, following Breedlove (1986), Martínez et al., (1994), Ibarra-Manríquez and Sinaca-Colín (1995, 1996a, 1996b) and Espinosa and Sarukhán (1997), by local botanists and professional taxonomists who had expert knowledge of the area. Species vouchers are available from the authors. Based on the literature cited above, each seedling was identified to species or genus level, and categorized into one of the following groups: pioneer, non-native (alien weeds and graminoids in the study area), and other forest species. A group of unidentified morphospecies was also included. Subsequent analyses were completed based on these groups.

Pioneers (*sensu* Swaine and Whitmore 1988) were recognized as those woody plants that establish only in open disturbed areas, and which are short-lived (< 40 yr), fast-growing, and reproduce copiously. The group “other forest species” included forest herbs, climbers and woody lianas, which were combined as they were too low in number to consider as separate groups. Weeds and graminoids were recognized as cosmopolitan herbs, shrubs or grass-like species, commonly associated with human-managed areas, which grow and reproduce aggressively. In the present study, we refer to both groups (i.e. ‘weeds’ and ‘graminoids’) as non-native plants (*sensu* Espinosa and Sarukhán, 1997).

Data analysis. A non-metric multidimensional scaling (NMDS) ordination was performed to evaluate soil seed bank similarity in terms of the abundance of species among sites and habitats. For this procedure, species abundance at each site was used to obtain a Bray-Curtis similarity matrix (Beals, 1984; McCune and Mefford, 1999). Abundance data were converted to a logarithmic scale to avoid any bias resulting from disparate abundance differences among species. A separate analysis was conducted for each plant group.

A Mantel test was performed to evaluate the effect, on species similarity, of distances among sites. We performed this test: i) between old-growth forest sites and ii) between pasture sites. The statistical significances of all Mantel correlations were assessed by Monte Carlo permutation tests, with 100 permutations. NDMS ordination and Mantel tests were carried out using PC-Ord ver. 4.36 (McCune and Mefford, 1999).

Generalized Linear Models (GLMs) in R 2.6.2 (Faraway, 2005; Crawley, 2007; R Development Core Team 2008) were used to assess differences in soil seed bank density between habitats and soil depths (layers). Analyses were conducted for i) total soil seed bank, ii) pioneers, iii) weeds, iv) graminoids, v) other forest species, and the

more abundant species from each plant group. We used GLMs, as their use is more appropriate when variance is not constant and when errors are not normally distributed, as was the case with our response variable (Faraway, 2005; Crawley, 2007). Due to the count nature of the dependent variable, Poisson error and a logarithmic link function were used. When over-dispersion occurred, we compensated by refitting the model using quasi-Poisson rather than Poisson errors (Faraway, 2005; Crawley, 2007). In models with this error and link function, the deviance explained by each term approximates Chi-square values and may be expressed as the percentage of the total deviance explained by each term (Faraway, 2005; Crawley, 2007). In these analyses, 'habitat' (2 levels: old-growth forest and pastures) was used as a discrete fixed factor with 6 replicates per level while 'layer' (2 levels: upper and lower) was used as nested factor within habitat. Bonferroni post hoc tests, to identify significant differences among treatments, were conducted when significant factor effects were detected (Faraway, 2005; Crawley, 2007).

To evaluate the invasion of non-native plants into the MABR, the relationship, between the soil seed bank density of weeds and graminoids in old-growth forest sites and the shortest distance to the Lacantun River, which represent the edge of the MAB reserve and the border of the agricultural areas, was explored through a regression

using the count data (Fig. 1). A GLM with Poisson error and a logarithmic link function was used. The procedures explained above for GLM analyses were also followed (Faraway, 2005; Crawley, 2007).

Soil seed bank in different tropical localities. To assess how the reduction of the pasture soil seed bank of pioneer species compared to that found in other studies, a relative index of pioneer seed availability in managed areas (PSA) was calculated and compared with the PSA of other localities. PSA was obtained by dividing the soil seed bank density of pioneer species recorded in a given pasture site by the soil seed density recorded in a neighbouring old-growth forest. Data from Uhl and Clark (1983), Aide and Cavellier (1994), Nepstad et al. (1996), Quintana-Ascencio et al. (1996), Wijdeven and Kuzee (2000), Uhl et al. (1981) and Uhl et al. (1982) were used. Finally, to assess how the invasion of non-native species into old-growth forest compared with other studies, we estimated the proportion of non natives (PNN) in the soil seed bank in the old-growth forest sites. We used the number of identified weeds and graminoids and the total soil seed bank density (including unidentified species), to avoid any bias in the PNN. Finally, our PNN was compared with those from other published studies (Uhl et al., 1982; Uhl and Clark, 1983; Nepstad et al., 1996; Quintana-Ascencio et al., 1996; Wijdeven and Kuzee, 2000; Brearley et al.,

Table 1. Statistics for soil seed bank density of different plant groups and species in 2 contrasting habitats at Montes Azules Biosphere Reserve and Marqués de Comillas Region, south-east Mexico. χ^2 and R^2 (in brackets) refers to the deviance and the proportion explained by each factor in the model, respectively. P values are provided and indicated with * when significant (see Fig. 3)

Plant Group-Species	Habitat (H)			Soil Layer (SL)		
	χ^2 and R^2	df	P	χ^2 and R^2	df	P
Total soil seed bank	22.2 (0.2)	1	<0.001*	8.4 (0.16)	2	<0.004*
Pioneer species	65.0 (0.43)	1	<0.001*	38.02 (0.25)	2	<0.001*
<i>Cecropia</i> sp.	55.1 (0.51)	1	<0.001*	31.6 (0.28)	2	<0.001*
<i>Acalypha machrostachya</i>	31.8 (0.58)	1	<0.001*	2.1 (0.04)	2	0.33
Weed species	27.7 (0.52)	1	<0.001*	4.7 (0.08)	2	0.09
<i>Vernonia</i> sp.	15.6 (0.47)	1	<0.001*	2.35 (0.07)	2	<0.31
<i>Calyptocarpus</i> sp.	0.2 (0.01)	1	<0.62	3.1 (0.16)	2	0.21
Graminoid species	45.1 (0.49)	1	<0.001*	28.1 (0.21)	2	<0.001*
<i>Fimbristylis dichotoma</i>	30.2 (0.48)	1	<0.001*	9.4 (0.15)	2	<0.001*
<i>Axonopus compressus</i>	8.76 (0.42)	1	<0.003*	1.89 (0.07)	2	<0.38
Other forest species	0.3 (0.01)	1	0.58	1.6 (0.04)	2	0.44
Unidentified	0.82 (0.02)	1	0.36	9.32 (0.33)	2	0.009

2004; Myster, 2004; Vieira and Proctor, 2007). To our best knowledge, these are the only published seed bank data available which include pioneers and non-native species in old-growth forest and agricultural sites.

Results

Seed bank community structure. In total, we recorded 4 597 seedlings across all soil samples, about 95% of which were at least identified to genus. Fifty-two morphospecies were recognized but only thirty were taxonomically identified; 16 to species and 14 to genus; fifteen of these taxa were weeds, 6 graminoids, 3 pioneers, while the rest belonged

to other forest species. The total number of morphospecies in the pasture and old-growth forest sites was 43 and 32, respectively. Due to the loss of the shade house to the above-mentioned flooding, 39% of the seedlings in the old-growth forest and 3% in the pasture sites could not be identified, (Appendix 2).

Among the total number of recorded seeds, pioneers represented more than 30% of the seed bank in the old-growth forest, but less than 1% in pastures, where almost the entire seed bank comprised seeds of graminoids and weeds (Fig. 2, Appendix 2). Pioneer species (*Cecropia* sp. and *Acalypha diversifolia*) were recorded among the 5 most abundant species in old-growth forest habitats, but also present were some graminoid weeds such as *Scleria pterota* and *Fimbristylis dichotoma*. The dominant species

Table 2. Seed bank density (seeds m⁻²) of rainforest tree species in old-growth forest (F) and agricultural (A) sites, and the relative index of pioneer seed availability (PSA = F/A) at different tropical forest localities: A) cases for pastures, B) cases for other agricultural uses. Soil samples were taken at the indicated soil depth (cm). With the exception of Santa Marta, Colombia, where seed bank density was obtained by a direct count of seeds, all other studies used the seed germination (seedling emergence) method. Different groups of trees recorded in the seed bank are indicated in parenthesis: 1) pioneer species, 2) *Cecropia* species, 3) all woody forest species

Locality	Depth	Forest (F)	Agriculture (A)	PSA (F/A)	Source
A) Pastures					
San Carlos, Venezuela (1)	5	171	46	0.27	Uhl and Clark, 1983
Santa Marta, Colombia (3)	1	~3000	~5	0.002	Aide and Cavelier, 1994
Paragominas, Brazil (1)	3	665	144	0.21	Nepstad et al., 1996
Chiapas, Mexico (3)	10	450	116	0.26	Quintana-Ascencio <i>et al.</i> 1996
Guanacaste, Costa Rica (3)	5	402	21	0.05	Wijdeven and Kuzee 2000
Chiapas, Mexico (1)	10	439	51	0.12	This study
B) Maizefields and yucca farms (*)					
San Carlos, Venezuela (1)	5	722	150	0.21	Uhl <i>et al.</i> 1981
San Carlos, Venezuela (2)	5	676	122	0.18	Uhl <i>et al.</i> 1981
San Carlos, Venezuela (3)*	5	168	47	0.27	Uhl <i>et al.</i> 1982
Chiapas, Mexico (3)	10	450	469	1.04	Quintana-Ascencio <i>et al.</i> 1996

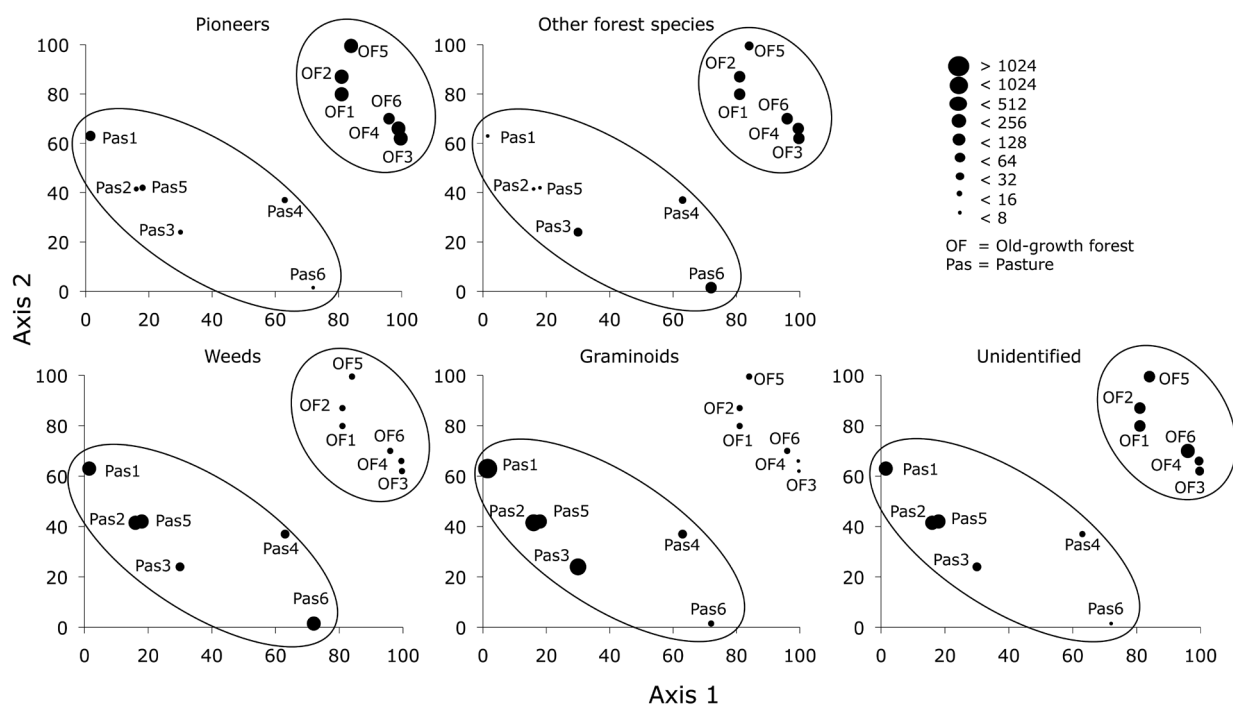


Figure 2. Soil seed bank community structure of old-growth forest (OF) and pasture sites (Pas) at Montes Azules Biosphere Reserve and Marqués de Comillas Region, southeastern Mexico, respectively. The NDMS ordination is completed per plant groups and shows the ordination between axis 1 and axis 2.

Table 3. Soil seed bank density (seeds m⁻²) of non-native plants (weeds and graminoids) and of the total seed bank in old-growth forest sites at different tropical localities. The proportion of seeds of non-native plants is shown in column PNN. Soil samples were taken at the indicated soil depth (cm). All studies used the seed germination method

Locality	Depth	Non-native	Total	PNN	Source
San Carlos, Venezuela	5	2	177	0.01	Uhl et al., 1982
San Carlos, Venezuela	5	0	200	0.00	Uhl and Clark, 1983
Paragominas, Brazil	3	28	700	0.04	Nepstad et al., 1996
Chiapas, Mexico	10	126	437	0.28	Quintana-Ascencio et al., 1996
Guanacaste, Costa Rica	5	254	1576	0.16	Wijdeven and Kuzee, 2000
Belem, Brazil	10	286	586	0.48	Vieira and Proctor, 2007
Luquillo, Puerto Rico	10	185	378	0.49	Myster, 2004
Maquipucuna, Ecuador	10	102	283	0.35	Myster, 2004
Kalimantan, Indonesia	5	47	175	0.27	Brearley et al., 2004
Chiapas, Mexico	10	346	2117	0.16	This study

of the pasture seed bank were graminoids, while the pioneer species *Ochroma lagopus* and *Cecropia* sp. occupied the 17th and 18th rank in abundance, respectively and represent <1% of the total density (Fig. 2, Appendix 2).

NMDS ordination of sites, based on species similarity and abundance, produced 2 clearly separate groups: old-growth forest and the pasture sites. The old-growth forest sites were very consistent and clearly grouped, while pastures were more dispersed. Ordination graphs for the plant groups clearly indicate different abundances among habitats: pioneers are more abundant in old-growth forest sites, while weeds and graminoids dominate the soil seed bank in pastures. Axis 1 of the ordination extracted 80.3% of the original distance matrix, axis 2 described 11.7% and axis 3 explained 4.5%, making the cumulative extraction for the first 3 axes 96.6% (Fig. 2.). Mantel tests for distance

correlation was significant ($r = 0.57$, $p = 0.05$) between old-growth forest sites but not between pasture sites ($r = 0.19$, $p = 0.22$), indicating that part of the observed variation in old-growth forest was due to distance, whereas in the pastures, site variation was unrelated to distance.

Overall, soil seed bank density was significantly (and more than one order of magnitude) higher in pasture than in old-growth forest habitats. In both habitats the upper soil layer had significantly higher seed density than the lower one (Fig. 3, Table 1).

Soil seed density of pioneer species in pastures. The trees *Cecropia obtusifolia*, *C. peltata* and *Ochroma pyramidale*, and the shrub *Acalypha diversifolia* were the only pioneer species identified in all soil samples. Due to the fact that we could not unequivocally distinguish seedlings of the 2 *Cecropia* species, we combined and classified these seeds

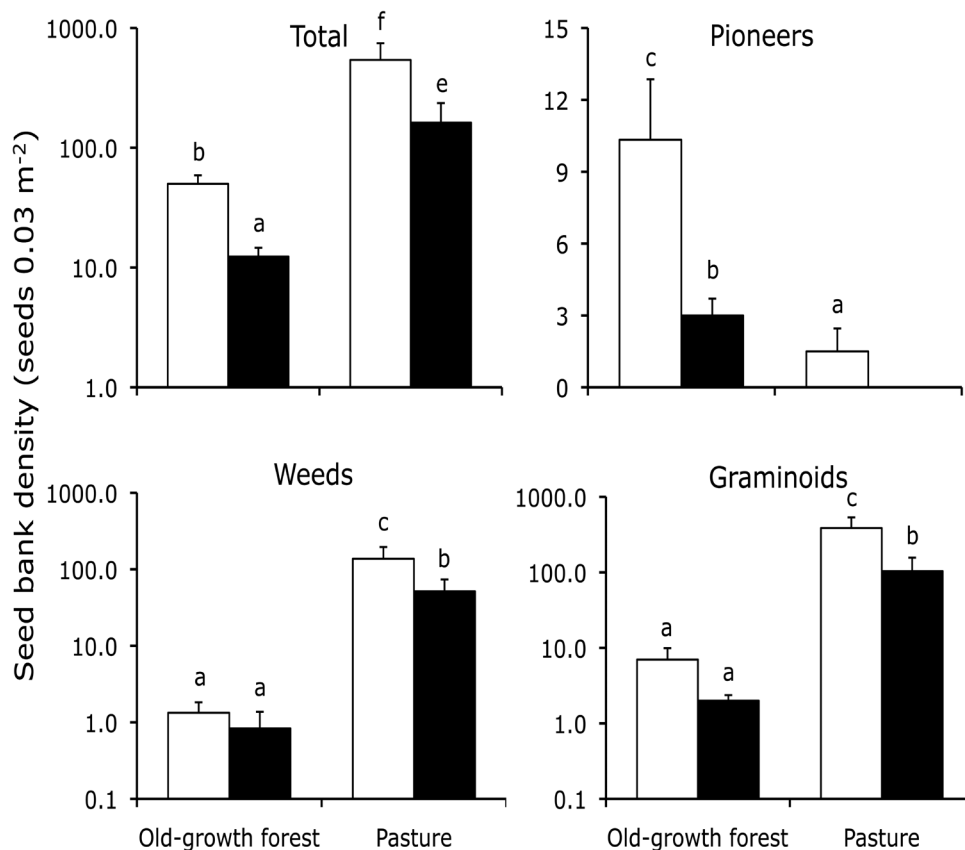


Figure 3. Soil seed bank density in old-growth forest sites at the Montes Azules Biosphere Reserve and pastures at Marqués de Comillas region, southeastern Mexico. Open and filled bars represent the upper (0-5 cm depth) and lower (5-10 cm depth) sampled soil layer, respectively. Bars which do not share a letter are significantly different ($P \leq 0.05$). Note the logarithmic scale in the Y axis in a), c) and d).

as *Cecropia* sp. for further analyses. Seed density of pioneer species was significantly lower (51 ± 32.6 seeds.m⁻²) in pasture sites than in the old-growth forest habitats (453.5 ± 53.1 ; Fig. 3). Seeds of pioneers in pastures were only found in the upper soil layer (Fig. 3). *Cecropia* was among the most dense seed taxa in old-growth forest habitats (323 ± 49); with a density 12 times higher than in pasture sites (28 ± 28). *Ochroma pyramidale* was only recorded in pastures. No pioneer shrubs were detected in the pastures (Appendix 2).

Weed invasion of the old-growth forest seed bank. Of the 21 non-native species (15 weeds and 6 graminoids) recorded in the pastures, 10 were found in the old-growth forest soil seed bank (Appendix 2). In the old-growth forest, the seed bank density of weeds, as well as of graminoids, was 2 orders of magnitude smaller than that found in pastures (Fig. 3; Appendix 2). Nonetheless, the high incidence of weeds (2%-4%), and particularly of graminoids (6%-28%), in the soil seed bank of old-growth forest was noteworthy (Fig. 3, Appendix 2). In the old-growth forest, seeds of both weeds and graminoids were similarly distributed between soil layers (Fig. 3).

The density of the soil seed bank of non-native species in the old-growth forest is related to distance from agricultural areas (Fig. 4). Specifically, a strong relationship between distance from agricultural fields (indicated by the Lacantun River) and density of weeds ($\chi^2 = 10.2$, df = 1, $P < 0.001$) and graminoids ($\chi^2 = 13.8$, df = 1, $P < 0.001$) was

found. This relationship was even stronger when weed and graminoid seeds were combined ($\chi^2 = 23.9$, df = 1, $P < 0.001$). Seeds of graminoids were found as far as 4 km from the edge of the Montes Azules reserve, represented by the Lacantun River and which represent the border of the agricultural areas (Fig. 4).

Soil seed banks in different tropical localities. Considering the 6 different studies in pastures, a low presence of pioneer seeds was found with a mean pioneer seed availability (PSA) of 0.15 (SE = 0.04). In our study, a PSA of 0.12 was found which concurs with the general trend (Table 2A). In the studies which included other agricultural uses, a 3-fold higher mean was found compared to that of pastures (PSA = 0.42, SE = 0.2) (Table 2B). The lowest value (0.002) was found in pastures located at Santa Martha, Colombia, while the highest (1.04) was found in maizefields from Chiapas, Mexico in a location very close to our study area. With the exception of 1 location (San Carlos, Venezuela), non-native plants were found to be present in the old-growth forest soil seed bank in each of the studies considered. The mean \pm SE of the proportion of non-native plants (PNN), of all the previous studies, was 0.22 ± 0.05 . This value was slightly higher than that found for our study site (PNN = 0.16). The lowest and highest PNN values of all studies were found at San Carlos, Venezuela (0.0) and Luquillo, Puerto Rico (0.49), respectively (Uhl and Clark, 1983; Myster, 2004; Table 3).

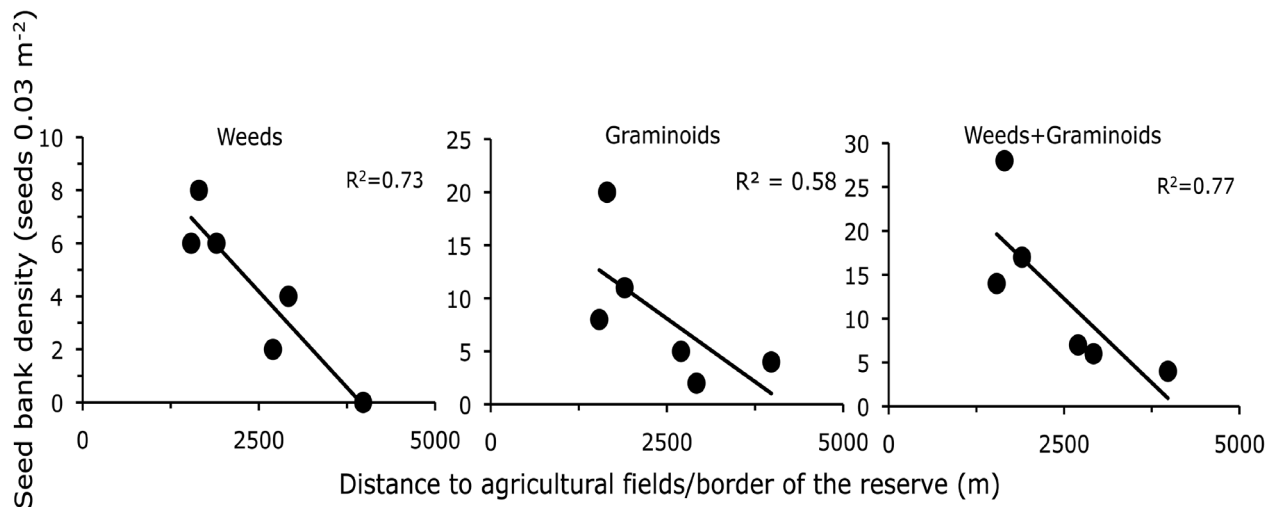


Figure 4. Relationship between soil seed bank density of non-native species (weeds and graminoids) in old-growth forest sites and distance (m) to agricultural fields/border of the reserve (represented by the Lacantun River edge). R^2 indicates the proportion of deviance explained by the term included in the model (distance) according to the GLM analysis (see Methods for explanation).

Discussion

Soil seed bank density of pioneer species in abandoned pastures. Overall, the seed bank of pioneer species was about 9 times lower in the pasture than in old-growth forest habitats. This low seed density may be associated with low seed rain, high seed predation, and/or high germination rates (Wijdeven and Kuzee, 2000; Esquivel et al., 2008; García-Orth and Martínez-Ramos, 2008). We do not believe that the unidentified seedlings in pastures (3%) modified this pattern, as these seeds germinated rather late and, in general, true pioneer species germinate, if conditions are suitable, during the first 18-30 days (Vázquez-Yanes and Smith, 1982).

The seed bank of pioneer species is very dynamic, as newly dispersed seeds continuously replenish the seeds lost through mortality or germination (Álvarez-Buylla and Martínez-Ramos, 1990; Dalling et al., 1998). When seed mortality/germination is not compensated by dispersal, seed bank density declines (Álvarez-Buylla and García-Barrios, 1993). Different studies have documented that seed rain density of pioneer species in pastures declines sharply with distance to the remnant forest; beyond 10-25 m from the forest edge the density tends to be marginal (Aide and Cavelier, 1994; Martínez-Garza and González-Montagut, 1999; Cubiña and Aide, 2001). Our studied pastures were at distances 25-250 m from forest fragments, and the low soil seed bank density of pioneer species was probably related to low numbers of dispersed seeds, particularly of the pioneer tree *Cecropia* (69% of all recorded pioneer soil seeds), for which more than 40 frugivorous animal species have been reported (Estrada and Coates-Estrada, 1984). Additionally, in our pastures there were no remnant trees, which have been documented to play an important role in attracting seed-dispersing animals (Guevara and Laborde, 1993). Other studies conducted in Marqués de Comillas have documented that seed rain density of *Cecropia* was very low in abandoned pastures; only 3.5 seeds m⁻² were caught in open pasture sites, a quantity 33 times lower than under isolated *Ficus* trees in the same pastures (García-Orth, 2008).

High seed predation rates may further reduce the soil seed bank of pioneer species in pastures (González-Montagut, 1966; Nepstad et al., 1996; Wijdeven and Kuzee, 2000; but see Aide and Cavelier, 1994). For example, in pastures in Marqués de Comillas, experimentally sown seeds of *Ochroma pyramidale* and *Cecropia obtusifolia* suffered 100 % removal by ants in only 8 days (García-Orth and Martínez-Ramos, 2008). In the same pasture sites, seedling emergence of these pioneer species was zero in the open pasture (García-Orth, 2008). Thus, low dispersal

and/or high seed predation rates may be the main factors accounting for the low density of pioneer species in the pasture seed bank. The fact that the pioneer species seed bank was confined to the top soil layer (0-5 cm) in pastures supports this idea, indicating that dormant seeds of pioneer species do not accumulate in the soil of pastures.

Regeneration consequences of a reduced seed bank of pioneer species. Reduced soil seed bank density of pioneer species may result in slower forest regeneration rates in abandoned pastures than in agricultural fields. Ongoing research in our study area indicates that the rate of recovery of stem density and basal area of woody vegetation (stems with dbh > 1 cm) was 6 to 8 times slower in pastures than in maize fields during the first 2 yr following abandonment (Martínez-Ramos et al. unpubl. data). Furthermore, the most abundant pioneer species in old-growth forest gaps were very rare or absent from the regenerating plant communities in pastures (García-Orth, 2008).

How does our estimate of reduction of the soil seed bank density of pioneer species in pastures compare with other studies with similar methodologies? Taking all cases into account, the average availability of soil seeds of pioneer species in pastures is 85% of that in nearby old-growth forest. However, there was a wide PSA variation among cases (0.002-0.27, Table 2). Pastures in Santa Marta (Colombia), and Guanacaste (Costa Rica) had soil seed banks which were much poorer in terms of pioneer species than our studied pastures. In contrast, in pastures in San Carlos (Venezuela), Paragominas (Brazil) and another locality in Chiapas (Mexico), seed availability of pioneer species was approximately double than that of our study locality (Table 2). Different levels of deforestation and fragmentation, combined with differences in land-use history, result in changes in the density of pioneer species seeds in pasture soils (Nepstad et al., 1996). At Marqués de Comillas, contemporary agricultural activities have occurred for no more than 35 yr, and a matrix of forest (old-growth and secondary forests) still covers about 50% of the land surface (Zermeño, 2008). Moreover, this area borders the 340,000 ha Montes Azules Biosphere Reserve. This landscape structure contrasts with the strongly fragmented forest matrix and long history of land management found in Santa Marta, Colombia (Aide and Cavelier, 1994), and with the long land-use history in Guanacaste, Costa Rica (Sánchez-Azofeifa et al., 2001).

Other agricultural land uses are less harmful to the soil seed bank of pioneer species than pasture. For example, maizefields close to our study area in Chiapas (Selva Lacandona region) had a PSA value 1 order of magnitude higher than that estimated for pastures (Quintana-Ascencio et al., 1996). In Chiapas, maizefields are frequently cultivated using traditional methods characterized by low-

intensity soil management techniques, and comprise small cultivated areas embedded in a forested matrix (Diemont et al., 2006), which may favour the arrival of seeds of pioneer species (Quintana-Ascencio et al., 1996; Levy and Aguirre, 2005).

Seed bank of non-native species in pastures. The major components of the seed bank in pastures were graminoids and weeds, which concurs with the results from other studies (Uhl and Clark, 1983; Wijdeven and Kuzee, 2000). In our case, almost 100% of seeds in the soil were from these types of plants. Pasture management probably affects the composition and abundance of the soil seed bank of weeds and graminoids. Several studies have indicated the importance of pasture management on tree regeneration in tropical pastures (Esquivel et al., 2008). For example, cattle management and the frequent use of fire probably deplete the seed bank of pioneer species, and inhibit forest regeneration (Aide and Cavelier, 1994; Miller, 1999; Esquivel et al. 2008). In some cases, fire is used to renew grass vegetation and to control weeds in tropical pastures (Uhl and Buschbacher, 1985). However, in other areas, there is evidence that this practice may have opposite effects and actually facilitate the growth of weed populations (D'Antonio, 2000; Wilson and Mudita, 2000). It is therefore possible that some of the attributes of our pastures, such as pasture isolation, fire frequency and cattle stocking density might have influenced the variation of the soil seed bank density of non-native species among the 6 studied pastures (Appendix 1). However, our design did not permit us to conduct any further analysis and this question must remain open for future research.

The high seed bank density of weeds and graminoids in pastures may have potentially important negative economic and ecological consequences. First, the development of large populations of these plants reduces pasture productivity (Nepstad et al., 1996; Méndez-Bahena, 1999). Secondly, after pasture abandonment, the weedy vegetation may deflect or arrest secondary forest succession (Nepstad et al., 1996; Martínez-Garza and González-Montagut, 1999; Méndez –Bahena, 1999; Esquivel et al., 2008). Weedy vegetation may inhibit forest regeneration even though abundant seeds of native plants disperse into the disturbed areas (Dalling and Denslow, 1998). In our study area, for example, the bracken fern, *Pteridium aquilinum*, aggressively invades areas where fire is frequently employed; covering large areas of pastures, even those which are completely surrounded by primary forest (Suazo, 1998).

Invasion of old-growth forest by seeds of non-native species. Our results document an important case of invasion of old-growth forest by seeds of non-native species from neighbouring agricultural areas, for example,

Fimbristylis dichotoma and *Scleria pterota*. We also found that this invasion extended at least 4 km into the MABR territory. It should be borne in mind that the Lacantun River is very wide (150 m) at the study site, and as such it is very likely that this river represented an important barrier to the spread of non native species from the MCR into the MABR. It would therefore be reasonable to expect even greater levels of invasion in areas with an absence of such barriers. However, certain weeds are wind-dispersed and they can reach areas further away (Wilson and Mudita, 2000; Kohli et al., 2006).

It is likely that the non-native seeds we recorded resulted from present or past human activities within the reserve. However, several lines of evidence refute this possibility: First, in the whole south-east area of the MABR there has not been an important human occupation since the Spaniards eradicated the Lacandon people, who lived in the area 315 yrs ago (De Vos, 1991). Secondly, forested areas within the MABR that were occupied in the past by Mayan settlements (indicated by abundant clay pottery) are free of such exotic species; instead forest herb species dominate the understorey (Martínez-Ramos *unpub. data*). Thirdly, the clear relationship between the density of seeds of non-native species in the soil seed bank of old-growth forest and the distance from agricultural fields strongly supports a process of front-like species invasion.

The presence of weeds and graminoids in the old-growth forest soil seed bank has been documented in other tropical localities at even higher proportions than found at our study site (see Table 3). For example in Belem, Brazil, more than 45% of the soil seed bank was composed of weeds or graminoids. This region is the oldest agricultural frontier in Amazonia and the landscape is dominated by secondary forest (Vieira and Proctor, 2007). This situation might be responsible for such a high density of weeds in the soil seed bank of old-growth forest sites. While the proportion of non-native species in our study site was not as high as found in other studies (see Table 3), it still suggests the importance of monitoring the invasive species in old-growth forest of Montes Azules Biosphere Reserve.

The invasion of old-growth forests by weeds from agricultural areas is well documented (Uhl et al., 1981; Quintana-Ascencio et al., 1996; Brearley et al., 2004). Their invasive capabilities are well illustrated by the case of tropical American invasive weeds, such as *Parthenium hysterophorus*, *Ageratum conyzoides*, *Lantana camara* and *Eupatorium odoratum*, in some rain forests in India (Kohli et al., 2006). Given their heliophyl character these weeds grow aggressively in forest canopy gaps and can interfere with the regeneration of forest species, causing adverse ecological, economic, and social impacts (Wilson and Mudita, 2000; Kohli et al., 2006). In our study, the reported

invasion is of great concern because it occurs in one of the core zones of the Montes Azules Biosphere Reserve (MAB-UNESCO), which is the largest tropical rain forest reserve in Mexico, and is apparently very well conserved. Nonetheless, extensive agricultural areas are located immediately adjacent to the core zone (separated only by the Lacantun River) and these may represent a significant risk to forest biodiversity, as forest gaps or forest edges represents disturbances which may offer suitable habitat for non-natives.

Our study system illustrates a case where pasture use has extensively depleted the soil seed bank of pioneers, while increasing the presence of non-native species. Land use, particularly pasture management, could be of greater detriment to the pioneer species within the soil seed bank leading to a reduction in forest regeneration rates once pastures are abandoned.

We believe that, following abandonment, the pastures of the Marqués de Comillas region represent a source of invasion by seeds of species non-native to the Montes Azules Biosphere Reserve, rather than a potential source of forest regeneration. The invasion of seeds of non-native plants as far as 4-km into the Montes Azules Biosphere Reserve highlights the need for improved planning for biological reserves in order to avoid the development of agricultural areas near the core zones of reserves. As has been suggested, pastures should be conceived as silvopastoral systems integrated into a strategy of multiple use in which fragmented forests, enriched secondary forests, and agroforestry can be combined to achieve productivity, conservation, and ecosystem service goals (Harvey et al., 2008). The results of this study emphasize the importance of monitoring invasive species within the boundaries of the Montes Azules Biosphere Reserve, the largest tropical rain forest reserve in Mexico.

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Appendix 1. Attributes of the 6 pasture sites studied in the Marqués de Comillas region (MCR), south-east Mexico. All pastures had less than 1 y of abandonment.

<i>Pasture site</i>	<i>Time of use (yr)</i>	<i>Cattle stocking density (ha⁻¹)</i>	<i>Cattle rotation period (d)</i>	<i>Average distance to remnant forest (m)</i>	<i>Fire frequency (fires in the last 8 yrs)</i>
Chajul 1	14	2	28-30	31	3
Chajul 2	15	1	10-12	40	1
Loma Bonita 1	13	2	15-18	243	2
Loma Bonita 2	11	7	29-30	248	2
Playón de la Gloria 1	12	5	28-30	85	4
Playón de la Gloria 2	9	2	18-30	47	1

Appendix 2. Seed bank density (seeds.m², 10 cm depth) for identified taxa recorded in old-growth forest and pastures sites at Montes Azules Biosphere Reserve and Marques de Comillas region, Selva Lacandona region, Mexico. Species are arranged by Plant group and then for family and species. **Cecropia* includes *C. obtusifolia* y *C. peltata*.

<i>Plant Group</i>	<i>Species</i>	<i>Family</i>	<i>Old-growth forest</i>	<i>Pasture</i>
Pioneer	<i>Ochroma pyramidale</i> Swartz	Bombacaceae	--	28 ± 28
Pioneer	<i>Cecropia</i> sp.*	Cecropiaceae	323 ± 49	23 ± 11
Pioneer	<i>Acalypha diversifolia</i> Jacq.	Euphorbiaceae	130 ± 28	--
OFS	<i>Tradescantia</i> sp.	Commelinaceae	51 ± 21	6 ± 6
OFS	<i>Sicydium</i> sp.	Cucurbitaceae	6 ± 6	--
OFS	<i>Xiphioidium coeruleum</i> Aubl.	Haemodoraceae	6 ± 6	--
OFS	<i>Hiraea</i> sp.	Malpighiaceae	6 ± 6	6 ± 6
OFS	<i>Acacia hayesii</i> Benth.	Mimosaceae	23 ± 17	--
OFS	<i>Gouania</i> sp.	Rhamnaceae	11 ± 7	--
Weed	<i>Amaranthus hybridus</i> L.	Amaranthaceae	11 ± 11	1446 ± 815
Weed	<i>Iresine</i> sp.	Amaranthaceae	--	2046 ± 1187
Weed	<i>Iresine celosia</i> L.	Amaranthaceae	--	85 ± 49
Weed	<i>Calypocarpus</i> sp	Asteraceae	17.0 ± 8	11 ± 11
Weed	<i>Eupatorium</i> sp	Asteraceae	6 ± 6	945 ± 485
Weed	<i>Melampodium divaricatum</i> (Rich.) DC.	Asteraceae	--	471 ± 192
Weed	<i>Vernonia</i> sp.	Asteraceae	6 ± 6	646 ± 342

Appendix 2. Continues

<i>Plant Group</i>	<i>Species</i>	<i>Family</i>	<i>Old-growth forest</i>	<i>Pasture</i>
Weed	<i>Euphorbia</i> sp.	Euphorbiaceae	11 ± 7	6 ± 6
Weed	<i>Phyllanthus niruri</i> L.	Euphorbiaceae	--	385 ± 268
Weed	<i>Desmodium</i> sp.	Fabaceae	6 ± 6	17 ± 17
Weed	<i>Sida acuta</i> Burm. f.	Malvaceae	--	159 ± 71
Weed	<i>Sida collina</i> Schltld.	Malvaceae	--	23 ± 23
Weed	<i>Conostegia</i> sp.	Melastomataceae	--	79 ± 53
Weed	<i>Rivina humilis</i> L.	Phytolaccaceae	17 ± 8	96 ± 47
Weed	<i>Lycianthes</i> sp.	Solanaceae	--	6 ± 6
Graminoids	<i>Cyperus</i> sp.	Cyperaceae	6 ± 6	11 ± 11
Graminoids	<i>Fimbristylis dichotoma</i> (L.) Vahl	Cyperaceae	170 ± 104	11304 ± 4382
Graminoids	<i>Scleria pterota</i>	Cyperaceae	91 ± 42	561 ± 268
Graminoids	<i>Axonopus compressus</i> (Sw.) P. Beauv.	Poaceae	--	2447 ± 1970
Graminoids	<i>Axonopus purpusii</i> (Mez) Chase	Poaceae	--	147 ± 84
Graminoids	<i>Eleusine indica</i> (L.) Gaertn.	Poaceae	--	2188 ± 728
Unidentified	--	--	657 ± 349	680 ± 448
Total	--	--	1653 ± 340	23855 ± 9459