



Intra and inter-annual variation in seed rain in a secondary dry tropical forest excluded from chronic disturbance

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ABSTRACT

Domestic livestock grazing and firewood extraction are chronic and pervasive disturbances in dry secondary forest that reduce diversity and modify composition. Exclusion of such disturbances may allow the reestablishment of original diversity. To investigate potential vegetation recovery following 30 years of perturbation, seed rain was evaluated monthly during 3 years in 96 0.78 m² seed traps located in eight exclosures established in 2006 in a species-poor secondary dry forest in central Mexico. Twelve additional seed traps were located outside the exclosures in 2010 for comparison purposes. Baseline diversity of seed sources (trees, ≥ 5 cm DBH) was recorded to compare standing tree composition with seed rain. Also, baseline diversity of potential primary (birds) and secondary (ants) dispersal vectors were registered to infer current plant–animal interactions. Total seed rain over 3 years within the exclosures comprised 180,375 seeds from 61 woody species, an average of 1.12 seeds/m²/month. Half of these species (31) and 95% of the seeds falling within the exclosures belonged to trees typical of perturbed sites. Sixty percent of all recorded seeds belonged to an early-successional, bird-dispersed shrub (*Hamelia patens* Jacq., Rubiaceae). Seed rain at one non-excluded plot was dominated by the wind-dispersed early-successional tree *Heliocarpus* sp. (Tiliaceae). Richness and seed density increased significantly in the second year of exclusion; however, by the third year, richness remained constant while seed density decreased. Seed rain was richer and more abundant during the dry season and was dominated by wind-dispersed species. Phenology, successional status and the dispersal modes of woody species explained most variance in richness and seed density of seed rain in early-successional dry forest. Seeds of early-successional species were dispersed in equal measure by abiotic and biotic vectors, whereas biotic vectors dispersed a higher density of late-successional seeds. The amount and timing of fall of abiotically dispersed seeds of the three most abundant species in the standing tree community may prolong their current domination of the landscape. However, even when richness in the seed rain within exclosures remained constant through time, composition was gradually shifting towards animal-dispersed species which may start a positive feedback producing an increase in animal visitation and a further increase of richness.

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1. Introduction

Secondary forest, resulting from succession following abandonment of agricultural land, currently covers more area than mature forest in the tropics (FAO 2004 in Chazdon et al., 2007) and in these secondary forest, studies continue to document pervasive chronic disturbance (e.g., West Africa, Nansen et al., 2001; Bolivia, Kennard, 2002; Mexico, Gonzalez-Iturbe et al., 2002; Romero-Duque et al., 2007; Hawaii, VanderWerf, 2004). Secondary forests are used for

the extraction of wood and for livestock grazing, with cattle ranching being the most destructive disturbance (Carranza-Montano et al., 2003; Monroy, 1997). This disturbance results in lower diversity and density of trees (Stern et al., 2002) and it also affects the native animals that interact with vegetation, such as birds (Martin and McIntye, 2007) and insects (Rambo and Faeth, 1999). After many years of disturbance, forest composition may totally change (Roth, 1999). Anthropogenic disturbances in the secondary dry forest impede the natural processes of recovery of flora and fauna to their former levels.

In successional areas, resprouting of vegetation diminishes after many years of continuous disturbance while the seed bank experiences high levels of predation (review in Ceccon et al.,

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2006). The arrival of forest species from dispersal events is therefore crucial for recovery of the former vegetation (Vieira and Scariot, 2006). Also, the potential advantage of certain species in highly seasonal ecosystems may be revealed by the timing of their fall (i.e. close to the onset of the rainy season; Vieira et al., 2008). The influx of forest species and their further establishment into successional areas is affected by phenology, dispersal modes and, presence and abundance of suitable dispersers, life history of tree species and distance to seed sources (old-growth forest). Most tropical dry forest species set flowers and fruits during the dry season (Kushwaha et al., 2011; Janzen, 1967; Borchert, 1996; Ceccon and Hernandez, 2009). Many tropical dry forest tree species are wind dispersed (Gentry, 1995) even though most species in tropical forests have fleshy fruits adapted for animal dispersal (Howe and Smallwood, 1982). Species dispersed by wind have light fruits that ripen during the dry season (Justiniano and Fredericksen, 2000); many of these species are early-successional pioneers able to establish in perturbed sites (Janzen, 1988). Species dispersed by animals are early- and late-successionals, with fleshy fruits that ripen either during the wet or dry season (Justiniano and Fredericksen, 2000; Vieira and Scariot, 2006). Wind-dispersed species with small seeds may be transported long distances by wind currents over open areas (see Bacles et al., 2006), but most of them fall within a few meters from the parent tree (e.g., Burrows, 1986; Augspurger and Franson, 1987); animal-dispersed seeds arrive at a given area when their vectors (i.e. birds, mammals) are attracted there, and seed distribution depends on animal behavior (see Griscom et al., 2007; Ceccon et al., 2006). Therefore, given that most forest animals avoid open areas, wind-dispersed pioneer species often are the first to arrive and dominate early-successional environments.

In this study, we evaluate richness and density of woody species in the seed rain over 3 years in a 30 year old secondary tropical dry forest at Sierra de Huautla, state of Morelos, central Mexico, to evaluate potential vegetation recovery after exclusion of chronic disturbance. Evaluating seasonal patterns of seed rain in recently excluded sites facilitates the understanding of the first filter of community assemblage (dispersal filter), following the cessation of disturbance events. We addressed the following questions: (1) Does richness and density of woody species increase in the seed rain with time of exclusion? (2) Does the monthly pattern of seed rain change with time of exclusion? (3) Does seed rain change from domination of wind dispersed and early-successional species to animal dispersed and late-successional species with time of exclusion? (4) Is seed rain affected by the interaction of time after exclusion, phenology, mode of dispersal and life history of the species falling within exclosures? and (5) Does seed rain differ in sites after 3 years of exclusion compared to a non-excluded site?

We had the following corresponding hypotheses: (1) there will be an increase in richness and density in the seed rain with time of exclusion, mainly due to an increase in vegetation cover and structure within the exclosures, (2) monthly pattern of seed rain will be independent of time of exclusion, most species and seeds will fall during the dry season, (3) amelioration of harsh abiotic conditions (i.e., high light levels, low water availability and little canopy cover in open areas) within exclosures with time will attract frugivorous animals from nearby old-growth forest, increasing fall of animal-dispersed and late-successional species and seeds, (4) The composition of seed rain within the exclosures will change with time from one dominated by wind-dispersed early-successional species to one of high richness of early- and late-successional animal-dispersed species irrespective of phenology, (5) seed rain outside the exclosures will remain dominated by early-successional species dispersed by wind.

2. Methods

2.1. Study site

This study was carried out on land close to the town of El Limón de Cuauchichinola (1220 m above sea level) located within the Sierra de Huautla Biosphere Reserve (SHBR), south of the state of Morelos, central Mexico. The SHB reserve (18° 20' 10", 18° 34' 20" N and 98° 51' 20", 98° 08' 15" W) contains 59,030 ha where the main vegetation type is tropical dry forest. Mean annual temperature is 24.5 °C and average total rainfall (average for 1971–2000) is 817.5 mm (CONAGUA, Gerencia Regional Balsas, <http://smn.cna.gob.mx/climatologia/normales/estacion/mor/NORMAL17057.TXT>), with ~90% of this falling between late May and October. During the dry season (November–April), most of the trees shed their leaves. Soils are shallow (<30 cm in depth), and are sandy-loam in texture.

In the SHB Reserve, 939 native species of vascular plants, from 478 genera and 130 families, have been registered (Dorado et al., 2005a) of which 157 species are trees or shrubs (Ramírez, unpublished data). This forest has one stratum of trees 8–12 m in height with convex or flat canopies; most leaves are compound with small leaflets (Rzedowski, 1978). The most important families in terms of species number are: Fabaceae, Poaceae, Asteraceae and Burseraceae. The most common canopy trees are *Conzattia multiflora* (B.L. Rob.) Standl., *Lysiloma acapulcense* (Kunth) Benth., *Lysiloma divaricatum* (Jacq.) J.F. Macbr. (Fabaceae), *Bursera* spp. (Burseraceae) and *Ceiba* spp. (Bombacaceae) (Dorado et al., 2005a).

2.2. Land history and description

The SHBR landscape is a mosaic of primary and secondary dry tropical forest surrounded by agricultural land and small towns. The 41.4% of the area in the SHB Reserve has been classified as intact or under good conservation status and the 22.4% was classified as well conserved based in aerial images and vegetation surveys in selected points; the remaining 36.2% show different degrees of degradation and most of it is used for economic activities (Trejo and Dirzo, 2000; Dorado et al., 2005a). In El Limón de Cuauchichinola, large parts of the forest were cleared >30 years ago, used for maize cultivation for ca. 6 years, and subsequently abandoned. Since then, the secondary forest has been used for wood extraction and extensive cattle ranching. Currently, in El Limón de Cuauchichinola, 56% of the area is covered with intact forest or under good conservation status, 19% with perturbed dry forest, 12% has secondary vegetation and the remaining 13% is dedicated to agriculture and housing (De Leon, 2005). In this forest, approximately 50% of organic matter is concentrated within the upper 10 cm of the soil profile (Solís, unpublished data). During the rainy season ca. 600 heads of livestock feed in this secondary forest (~7 head/ha), most of which are brought from neighboring towns. Cattle are maintained in farms during the dry season but goats, pigs and horses are left to forage in the forest daily throughout the year (Maldonado, unpublished data; Gerardo Pacheco, personal communication). As a part of an experimental restoration project which aims to promote the coexistence of cattle grazing activities and forest biodiversity, eight 50 × 50 m plots were excluded from perturbation in the form of wood extraction and grazing by large domestic livestock since January 2006. Exclusion was accomplished with a fence of 4 lines of barbed wire, with an additional 75 cm of chicken wire netting attached to the lower part of the fence to exclude smaller domestic animals. The fences still allowed native herbivores, including deer (*Odocoileus virginianus*) and rodents (*Lyomys irroratus*, *Baiomys musculus*, *Sigmodon hispidus*; Valenzuela-Galván, unpublished data) to access the excluded

areas. Even with the presence of the chicken wire, some soil removal by domestic pigs was recorded in one plot. Distance among exclosures ranged from 0.08 to 1.59 km (0.72 ± 0.46 ; mean \pm standard deviation). The closest old-growth forests were located in a range from 0.11 to 0.26 km ($0.21 \text{ km} \pm 0.05$) from exclosures.

2.3. Initial biodiversity

To have baseline data of diversity associated with the local seed sources and their main potential primary (bird) and secondary (ants) dispersal vectors, we recorded the tree species, and the bird and ant diversity. All woody vegetation with ≥ 5 cm diameter at breast height (DBH; 1.3 m) was tagged and measured in May 2006 and with these data, richness, density and basal area were calculated. Thirty-three woody species from 14 families were recorded, with a density of 252.5 trees/ha and basal area of 6.18 m²/ha. Fifty-one percent of the tree species recorded had fleshy fruits to be dispersed by animals while 81% of the individuals recorded had dry fruits for wind or gravity dispersal. The most abundant species were *Acacia cochliacantha* (Fabaceae, 75 trees/ha), *Ipomoea pauciflora* (Convolvulaceae, 50 trees/ha) and *Mimosa bentharii* (Fabaceae, 31 trees/ha). *Ipomoea* accounted for 33% of the total basal area in this secondary forest (see Appendix Table A1).

A total of 3572 ants from four sub-families, 12 genera and 17 species were collected, an average of 0.18 ± 0.14 ants/m² (Agosti et al., 2000). Three seed harvester and omnivorous species (*Pogonomyrmex barbatus* and two *Pheidole* spp.) comprised 87% of all individuals. *Pheidole* spp. represented $\geq 51\%$ of all ants collected in each exclosure; the fourth most abundant species was *Solenopsis geminata*, also an important seed harvester (see Appendix Table A2). Harvester ants are primary dispersal vectors of myrmecophilous seeds (with elaiosome) and potential secondary dispersal vectors of all other small seeds (see for example Retana et al., 2004).

A total of 361 individuals of 31 species from 11 families of birds were recorded. Three bird species accounted for 41 percent of individuals: *Columbina inca* (Columbidae, $N = 61$ individuals), a granivorous species most commonly seen on the ground, followed by *Aimophila ruficauda* (Emberezidae, $N = 50$ individuals), which feeds on seeds and arthropods from the soil, and *Icterus pustulatus* (Icteridae, $N = 42$ individuals), a frugivorous “gulper” species. Fifty-five percent of the bird species, and 86% of the individuals recorded, eat and potentially disperse fleshy-fruited species (see Appendix Table A3).

2.4. Seed rain

Twelve seed traps were randomly located within each exclosure in early May 2006. To avoid potential cluster of the 12 seed traps in a small area of the 50 \times 50 m plots, location of half of the traps (6 traps) were done randomly in each half of the plot (25 \times 25 m). Seed traps consisted of a circular plastic tube shaping a ring of 1 m of diameter fixed to the ground with metal poles 75 cm in height, with a 50 cm deep cloth hanging from the plastic tube with a rock at the bottom of it. This rock allow the concentration of seeds at the bottom of the cloth, where seeds were not available to predators; also, grasses were cut around traps to prevent seed predators (mainly rodents) to climb seed traps. The 96 traps (total capture area 75 m²) in the exclosures were emptied monthly. This secondary forest does not have a continuous closed canopy; 40% of the traps were located in open areas or under a gap in the canopy. These seed traps capture species dispersed by wind, gravity and flying animals. Continuous destruction of the seed traps by domestic animals and removal of trap materials by people prevented us from maintaining seed traps outside exclosures during the entire period of study. However, we placed 12 additional seed traps in a

50 \times 50 m area in the secondary forest during the period when cattle density was lowest (i.e., cattle from neighboring towns were being taken back to farms) and highest richness and density of seed rain was recorded (i.e., dry season), and we were able to maintain these traps in position for 4 months (early January to end of April, 2010). Most tree seeds were identified with the use of the reference collection of the School of Biological Sciences, Universidad Autónoma del Estado de Morelos, (UAEM; Flores-Morales, unpublished data). The photographic seed collection of the Department of Evolutionary Ecology and samples from the Herbaria HUMO-UAEM served as photographic and physical reference collections. Data included here were of samples from exclosures collected between early June 2006 and May 2009. The successional status of species recorded in the seed rain was defined by the literature (see references in Appendices) and by a census carried out in old-growth forest (three 0.25 ha plots; Martínez-Garza, unpublished data; late-successional species) and secondary forest (2 ha of this study; early-successional species).

2.5. Statistical analyses

Two Repeated Measures Analyses of Variance (Zar, 1996), one for richness and one for density of seeds by (1) dispersal mode with two levels (biotic and abiotic), (2) month of dispersal with 12 levels (May–April), for 3 years (years after exclosure as the within-effect factor) were done. Due to the low density of late-successional species and seeds it was not possible to analyze the pattern of seed rain by successional status of species and their dispersal mode for 12 months during the 3 year period of study, instead, another two Repeated Measures Analyses of Variance were performed comprising the main factors described previously, but replacing month with season (two levels: dry and rainy season). Rainy season included May–October ($\sim 90\%$ of annual precipitation) and dry season included November–April (months with average precipitation ≤ 20 mm). Therefore, analysis regarding dispersal mode of species were performed twice, one analysis including 12 months of dispersal and one including two seasons of dispersal.

Variables were transformed with the natural logarithm plus one to comply with ANOVA assumptions. To recognize the most important sources of variation in the two ANOVAs, the percentage of variance explained (% VE) was calculated for each single factor and their interactions (Crawley, 1993). Averages and standard errors shown were back-transformed for clarity. Sorensen Similarity Index ($2C/A + B \times 100$; Krebs, 1989) was calculated with species composition of trees (A ; ≥ 5 cm DBH, Appendix Table A1) and seed rain for the 3 years (B ; Appendix Table A4), where C represent the number of species occurring in both groups; similarity index was also calculated separating species by dispersal mode. Medians of the density of seeds are shown for the non-excluded plot. All statistical analyses were performed in STATISTICA 7.0 (StatSoft, 2004).

3. Results

The seed rain over 3 years (2006–2009) in the eight exclosures included 180,375 seeds from 61 woody species, of which 8914 seeds of 31 species were late-successional. Sixty percent of all the seeds recorded in the 3 years were from the bird-dispersed shrub *Hamelia patens* Jacq. (Rubiaceae). The average seed rain was 1.12 seeds/m²/month over 3 years for all species (see Appendix Table A4). Seed rain at a non-excluded plot for 4 months in 2010 (January–April) contained 2288 seeds from 15 woody species, of which 258 seeds of five species were late-successionals. Sixty-eight percent of all seeds recorded in the non-excluded plot were from the wind-dispersed early-successional tree *Heliocarpus* sp. (Appendix Table A4).

3.1. Richness and density of woody species with time of exclusion

Overall, richness and seed density increased in the second year of exclusion (0.35 ± 0.01 species and 7.28 ± 0.07 seeds/m²/month respectively) and decreased by the third year (0.32 ± 0.01 species and 5.24 ± 0.06 seeds/m²/month respectively). Richness and seed density were significantly different by year (Table 1). A Post hoc Tukey test showed that richness and density of seeds increased significantly by the second year. By the third year, richness in the seed rain was similar to that in the first and second year while seed density decreased by the third year becoming indistinguishable from that recorded in the first year.

3.2. Monthly pattern of seed rain

Over the 3 years, the highest richness and seed density were recorded in December (0.56 ± 0.02 species and 99.01 ± 1.2 seeds/m²/month), the lowest richness in June (0.09 ± 0.02 species/m²/month) and the lowest seed density in July (0.60 ± 0.6 seeds/m²/month). Richness and seed density differed significantly by month (Table 1) and a post hoc Tukey test revealed similar high richness from November through to April (which coincides with the dry season), while seed density was significantly higher in November and December compared to all other months. Month of dispersal was the single factor that explained most of the percentage of variance of richness (12.7%) and seed density (25.5%; Table 1). The interaction of year after exclusion with month was significant for richness and seed density (Table 1). However, the post hoc Tukey test did not show relevant changes in the monthly pattern of seed rain for richness (Fig. 1a). For seed density it showed that significantly more seeds fell in October and November of the third year and during January, March and April of the second year (Fig. 1b).

3.3. Dispersal mode of species in the seed rain

Over 3 years, animals dispersed 115,876 seeds of 30 species over the sampled 75 m², while 64,499 seeds of 31 species were dispersed by wind or gravity within the same area (Appendix Table A4). Over the 3 years, an average of 0.36 ± 0.01 species and 5.15 ± 0.08 seeds/m²/month, dispersed by abiotic vectors, reached the exclosures while 0.29 ± 0.01 species and 5.94 ± 0.08 seeds/m²/month seeds, dispersed by biotic vectors, were recorded. A significantly higher richness dispersed by wind or gravity was recorded compared to richness dispersed by animals while the density of seeds dispersed by abiotic and biotic vectors was statistically similar (Table 1). The interaction of year after exclusion with dispersal

Table 1

Repeated measures analyses of variance of richness and seed density (seeds) over 3 years (May 2006–April 2009), by month (12 levels) and dispersal mode (Dispersal m; two levels: wind or gravity and animals [birds and bats]), and their interactions in the seed rain within eight exclosures in the dry secondary forest of Sierra de Huautla, Morelos, Mexico. Source of variation (Factor), degrees of freedom (df), *F* values and variance explained (VE; %) are shown.

Factor(df)	Richness	VE	Seeds	VE
Month ₍₁₁₎	34.8***	12.7	49.3***	25.5
Dispersal mode ₍₁₎	18.1***	0.6	1.2	0.0
Dispersal mode* month ₍₁₁₎	20.5***	7.5	6.4***	3.3
Error ₍₁₆₈₎				
Year ₍₂₎	5.4*	0.1	18.9***	0.5
Year* month ₍₂₂₎	2.3***	0.6	8.8***	2.5
Year* Dispersal mode ₍₂₎	1.4	0.0	3.4*	0.1
Year* month* Dispersal m ₍₂₂₎	3.7***	1.0	3.6***	1.0
Error ₍₃₃₆₎				

* $P < 0.05$.

*** $P < 0.0001$.

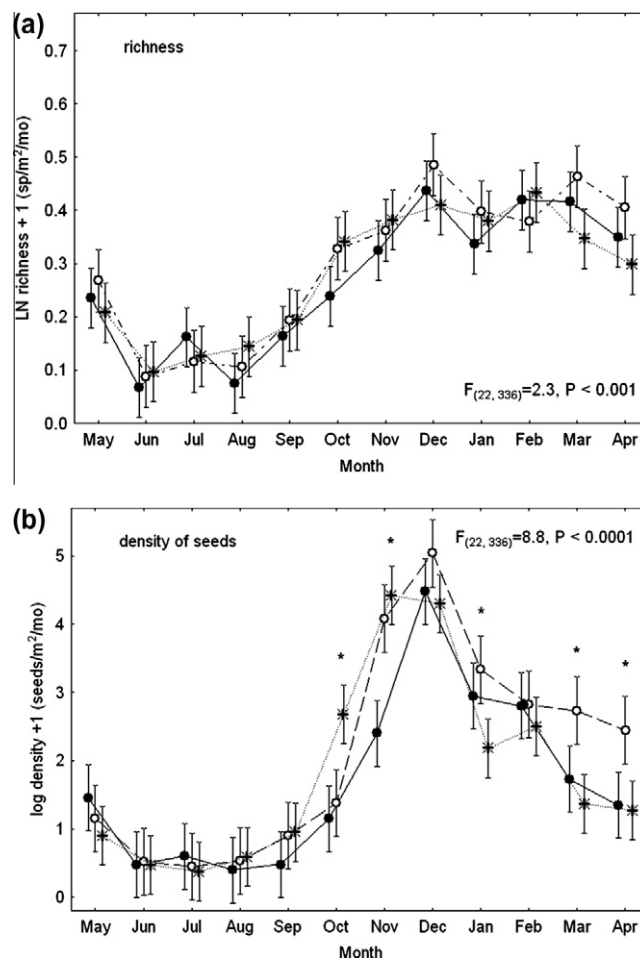


Fig. 1. Average of (a) natural logarithm of richness + 1 and (b) natural logarithm of density of seeds + 1 falling during year 1 (black dots continuous line), year 2 (open dots intermittent line) and year 3 (asterisks and dotted line) in 12 months within eight exclosures at a secondary dry forest in Sierra de Huautla, Morelos, Mexico. Vertical bars represent 95% confidence intervals. Stars indicate significant differences for density within months, tested with Post hoc Tukey test. Statistics indicate the interaction of month and year of exclusion for the response variable.

mode was not significant for richness, but it was for density of seeds (Table 1); however, the Post hoc Tukey test revealed that the densities of abiotically and biotically dispersed seeds were similar within years.

The similarity index between the composition of all standing trees within the exclosures (≥ 5 cm DBH, Appendix Table A1) and seed rain for the 3 years (Appendix Table A4) was 65%. When species were divided by dispersal mode it was found that for wind dispersed species similarity Index was 79% revealing that all but one wind-dispersed species standing in study site, plus seven additional immigrant species were represented in the seed rain. A lower similarity index of animal dispersed species was calculated (57%) revealing that all but five standing tree species were represented in the seed rain and additionally 13 tree species dispersed by animals not represented in the standing community were falling within exclosures (Appendix Tables A1 and A4).

3.4. Seed rain by season

On average, more species and eight times the number of seeds fell in the dry season (0.35 ± 0.01 species and 4.4 ± 0.2 seeds/m²/month), compared to those recorded in the rainy season (0.53 ± 0.01 species and 35.1 ± 0.2 seeds/m²/month). Richness and

seed density were significantly different by season (Table 2), and this was the single factor that explained most of the percentage of variance in richness (2.4%) in the seed rain. The interaction of year after exclusion with season was significant for seed density (Table 2), however, the Post hoc Tukey test revealed that the densities of seeds during the dry season were always significantly higher than that during the rainy season within the years.

3.4.1. Dispersal mode of species by season

The richness dispersed by abiotic and biotic vectors was statistically similar, while a significantly higher density of seeds dispersed by animals was recorded compared to density dispersed by wind (Table 2). The interaction of year after exclusion with dispersal mode was not significant for richness, but it was for density of seeds (Table 2). However, this interaction explained less variance (0.4%) than the one including also successional status (see below), and therefore the later is more relevant.

3.4.2. Successional-status of species by season

During the study period, 95% of seeds and nearly half of the species recorded (30 sp.) belonged to woody species usually found in perturbed sites (early-successional species) (Appendix Table A4). Overall, more early-successional (0.5 ± 0.01 species and 42.9 ± 0.2 seeds/m²/month) than late-successional species and seeds (0.4 ± 0.01 species and 3.4 ± 0.4 seeds/m²/month) arrived within the enclosures. Richness and seed density were significantly different by the successional status of species (Table 2). The successional status of species was the single factor that explained most of the percentage of variance in density of seeds (11.8%; Table 2). The interaction of years after exclusion with the successional status of species was significant for seed density (Table 2); however, the Post hoc Tukey test revealed that the densities of early-successional seeds were always significantly higher than that of late-successional seeds within the years.

3.5. Interactions among factors

Dispersal mode by month was the interaction that explained most of the percentage of variance in richness (7.5%) and density

of seeds (3.3%) (Table 1). Seed rain was dominated by animal dispersed species in September and October (end of the rainy season), whereas this pattern reversed in 5 months of the dry season, from December to April, when the richness of abiotically dispersed species was significantly higher than that of biotically dispersed ones (Fig. 2). This result was confirmed with the significant interaction of dispersal mode by season (Table 2). The Post hoc Tukey test revealed a significantly higher richness of animal dispersed species in the rainy season and a significantly higher richness of wind dispersed species in the dry season; this analysis also revealed that richness of animal dispersed species is similar in both seasons.

The interaction of the successional status of species and dispersal mode explained most of the percentage of variance in richness (12.1%) (Table 2). A significantly higher richness of early-successionals were dispersed by abiotic vectors than by biotic ones whereas a significantly higher richness of late-successionals were dispersed by biotic vectors. The interaction of season and the successional status of species was significant for richness and density. The Post hoc Tukey test revealed that during the dry season there were significantly more early-successional species falling whereas during the rainy season a similar average of early- and late-successional species were recorded in the seed rain. This

Table 2

Repeated measures analyses of variance of richness and seed density for 3 years (May 2006–April 2009), two seasons (dry and rainy), by successional status of species (Succession; early and late-successional species), dispersal mode (Dispersal m; two levels: wind or gravity and animals [birds and bats]) and their interactions in the seed rain within eight enclosures in Sierra de Huautla, Morelos, Mexico. Source of variation (Factor), degrees of freedom (df), F values and variance explained (VE; %) are shown.

Factor(df)	Richness	VE	Seeds	VE
Season ₍₁₎	48.4***	2.4	95.9***	8.1
Dispersal mode ₍₁₎	0.5	0.0	14.6**	1.2
Successional status ₍₁₎	22.7***	1.2	139.3***	11.8
Season* Successional status ₍₁₎	17.3***	0.9	57.7***	4.9
Season* Dispersal mode ₍₁₎	31.9***	1.6	1.2	0.1
Successional status* Dispersal mode ₍₁₎	240.4***	12.1	2.0	0.2
Season* Succ s* Dispersal mode ₍₁₎	4.9*	0.2	5.0*	0.4
Error ₍₅₆₎				
Year ₍₂₎	4.6*	0.2	16.1***	0.7
Year* Season ₍₂₎	1.8	0.1	6.7**	0.3
Year* Successional status ₍₂₎	1.3	0.1	12.9***	0.5
Year* Dispersal mode ₍₂₎	1.5	0.1	8.5***	0.4
Year* Season* Successional status ₍₂₎	2.3	0.1	5.2*	0.2
Year* Season* Dispersal mode ₍₂₎	1.4	0.1	4.2*	0.2
Year* Succ s* Dispersal mode ₍₂₎	3.3*	0.2	21.2***	0.9
Year* Season* Succ s* Dispersal mode ₍₂₎	2.9	0.1	6.3*	0.3
Error ₍₁₁₂₎				

* $P < 0.05$.

** $P < 0.001$.

*** $P < 0.0001$.

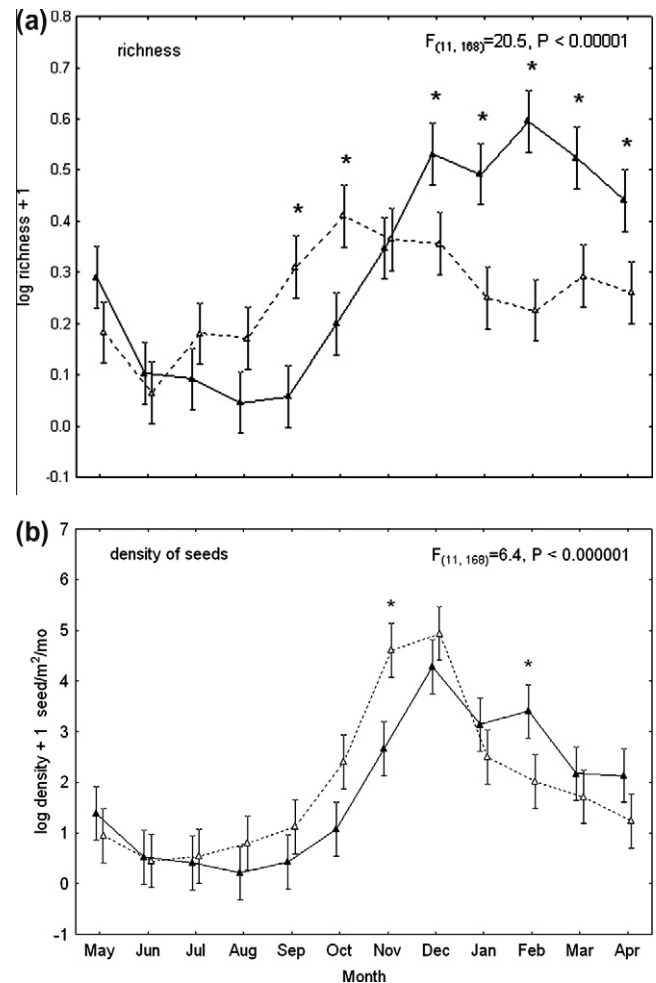


Fig. 2. Average of (a) natural logarithm of richness + 1 and (b) natural logarithm of density of seeds + 1 dispersed by wind (black triangles and continuous line) or animals (white triangles and intermittent line), in 12 months over 3 years within eight enclosures at a secondary dry forest in Sierra de Huautla, Morelos, Mexico. Vertical bars represent 95% confidence intervals. Stars indicate significant differences for the response variable within months, tested with Post hoc Tukey test. Statistics indicate the interaction of month and dispersal mode for the response variable.

interaction explained most of the percentage of variance in the density of seeds (6.2%) (Table 2); however, the Post hoc Tukey test revealed that more early-successional seeds were recorded at both seasons in the seed rain. It is relevant to note that richness and density of seeds of late-successionals were not affected by season.

The interaction of the year after exclusion, successional status of species and dispersal mode explained most of the percentage of variance in richness for the interactions of second degree (0.9%) (Table 2). The Post hoc Tukey test revealed that the density of early-successional seeds dispersed by wind were higher than those of late-successionals and remained in similar levels during the 3 years. On the other hand, the density of early-successional seeds dispersed by animals increased significantly by the second year and remained that high for the third year. The density of late-successional seeds dispersed by wind increased significantly by the second year and decreased by the third year whereas the density of late-successional seeds dispersed by animals remained in similar lower levels during the 3 years (Fig. 3).

The remaining interaction of second grade that was significant in the analysis by month (Table 1) explained 1% of variance in richness and 1% of variance in density of seeds. The remaining interactions of second and third grade that were significant in the analysis by season (Table 2) explained 0.4% of the variance in richness and 1.1% of the variance in density of seeds. Therefore, lower grade interactions or single factors were more relevant.

3.6. Seed rain in a non-excluded plot

In the seed rain recorded in the 12 seed traps located within one non-excluded plot, median seed density from January to April for the 15 species recorded was 35.8 seeds/m²/month. Median values inside exclosures, for the previous 3 years, from January to April for the 15 species recorded at the non-excluded plot, was 38.3 seeds/m²/month. Sixty-three percent of the tree species recorded in seed rain at the non-excluded plot was also found in the standing tree community (≥ 5 cm DBH; data not shown).

4. Discussion

Richness and seed density showed a regular monthly pattern and these variables showed a slight increase in the seed rain in a

species-poor secondary dry forest during 3 years of exclusion of disturbance. Early-successional wind-dispersed species dominated the seed rain, however a gradual shift to species dispersed by animals was noted with time of exclusion and in comparison to the seed rain falling in the non-excluded plot.

4.1. Time of exclusion

Exclusion of disturbance for 3 years in a species-poor secondary dry forest did not steadily increase richness and density of seeds contrary to expectations. Seed rain has been found to be higher under woody vegetation than in open areas (Willson and Crome, 1989; Slocum and Horvitz, 2000, for humid forest; Chimeria, 2004, for dry forest) and also, higher under taller trees compared to shrubs (Duncan and Chapman, 1999). These facts agree with chronosequences studies in cloud forest where higher seed density and richness in the seed rain of later successional areas (higher tree cover) was found compared to early successional areas (lower tree cover; del Castillo and Rios, 2008). Therefore, when areas without canopy cover, as open pastures or agricultural lands are excluded from anthropogenic disturbances, seed rain is expected to increase steadily with time of exclusion, initially close to or under the first woody vegetation colonizing. In the poor-species secondary dry forest of this study, exclusion of anthropogenic perturbation during 3 years allowed the development of an understory community with a biomass and richness similar to that of a more conserved forest (de la O-Torres, 2009), a higher recruitment of woody species compared with non-excluded sites (Alba-García, 2011) and the further development of the standing tree community (Martínez-Garza, 2010). Even though richness and seed density did not increase significantly with time of exclusion, changes in composition of the seed rain by the dispersal mode and the successional status of species were taking place. More than 50% of the animal-dispersed species falling in the seed rain were from species not present in the standing tree community within exclosures (see below).

4.2. Seasonal pattern

In accordance with our expectations, the highest richness and seed density in the seed rain was recorded during the dry season and this pattern was independent of time of exclusion. It has been repeatedly shown that in seasonal ecosystems, most species produce flowers and fruits during the dry season (Borchert, 1996; Grombone-Guaratini and Rodrigues, 2002; Justiniano and Fredericksen, 2000; De Leon, 2005; Ceccon and Hernandez, 2009; Mostacedo et al., 2001). Flowering may occur early in the dry season when many trees use the water they did storage in their trunks during all the rainy season plus the water they still can accede from the subsoil level (Borchert, 1994). Besides, for deciduous species, leaf shedding results in additional water availability for the release of flower buds (Borchert, 1996). Therefore, most species are ready to disperse their seeds during the dry season, 3–4 months ahead of the onset of rains.

Month (January–December) or season of dispersal (dry and rainy season) were the single factors that explained most of the variance in richness and density of seeds. However, studies in the region and in similar ecosystems in the Neotropics have shown that phenological patterns depend heavily on dispersal mode of species: wind-dispersed species produce fruits mainly during the dry season, while animal-dispersed species may fall during the dry and the rainy season (Borchert, 1996; Justiniano and Fredericksen, 2000; De Leon, 2005 but see Griz and Machado, 2001). The fall of most wind-dispersed species and seeds during the dry season expose them to predation and desiccation for longer periods of time (Vieira et al., 2008). However, this time in the seed bank also

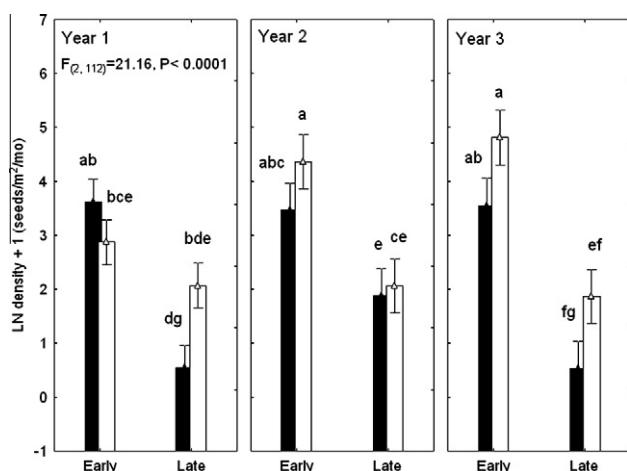


Fig. 3. Average natural logarithm of density of seeds + 1 of early- and late-successional species dispersed by wind (black columns) or animals (white columns) during 3 years within eight exclosures in Sierra de Huautla, Morelos, Mexico. Vertical bars represent 95% confidence intervals. Different letters indicate significant differences for density of seeds tested with Post hoc Tukey test. Statistics indicate the interaction of year, successional status of species and dispersal mode for density of seeds.

expose seeds to secondary dispersal (for example by ants; Dominiguez-Haydar and Armbrrecht, 2011) and, to the natural processes that break seed dormancy (Baskin and Baskin, 1998). Phenologies of seed rain dispersed by biotic and abiotic factors at this successional dry environment are extremely regular within years suggesting that most seeds spend *ca.* 4 months in the soil before the onset of rains for potential germination.

4.3. Dispersal modes

A higher proportion of wind-dispersed species and seeds are expected to fall in perturbed areas. In our plots, excluded from perturbation, analyses by month showed that wind-dispersed species still dominated the seed rain after 3 years; however a comparable amount of animal dispersed seeds (from less species) were falling within exclosures. When analyses were performed by season, analysis showed a similar richness of wind and animal dispersed species and a higher density of animal dispersed seeds. All available studies of seed rain in perturbed dry forest of the Neotropics have evaluated seed rain for less than 1 year and also show contrasting results: in a dry forest in Bolivia, a similar proportion of species and seeds dispersed by biotic and abiotic vectors were recorded in the seed rain during the dry season (6 months; Mostacedo et al., 2001) when the largest differences between dispersal modes are expected (see above). In a Hawaiian dry forest, a higher percentage of species and seeds of native and exotic species were dispersed by wind during 1 year study period (Chimera, 2004). Finally, a higher density of seeds belonging in 87% to species dispersed by abiotic vectors, were recorded during the dry season in a dry forest of Xochicalco, Morelos, Mexico during 1 year study period (Ceccon and Hernandez, 2009). Discrepancies in the proportion of dispersal modes of species in the seed rain may be due to shorter time spans evaluated, composition of standing vegetation and/or lack of plant interactions with biotic dispersal vectors.

Wind-dispersed seeds will fall close to parent trees whereas seed rain of animal-dispersed species will depend on animal behavior as well as composition and abundance of dispersal agents (Griscom et al., 2007). Poor dispersal of some plant species may be the result of the absence of key dispersal vectors (Loiselle and Blake, 2002; Kirika et al., 2008). Further, cattle may disturb fauna and their interactions with plants (VanderWerf, 2004; Martin and McIntye, 2007). For example, in a grassy eucalypt woodland in Australia, understory-dependent birds were those most affected by livestock grazing, resulting in species-poor bird assemblages dominated by a few bird species (Martin and McIntye, 2007). In the present study, three bird species accounted for 41% of individuals recorded, while 55% of species and 47% of individuals recorded are known to consume and potentially disperse fleshy-fruited species. By comparing compositions of species in the seed rain and standing vegetation, it was revealed that >50% of the animal dispersed species in the seed rain were from adults not present in the neighboring community (immigrant species, Martínez-Ramos and Sotocastro, 1993) whereas only 32% of the wind-dispersed species falling within plots were immigrants. Most wind-dispersed seeds are falling closer to parent trees while seed rain of animal-dispersed species reflects visitation of animals (i.e., frugivorous birds) to this habitat excluded from perturbation.

Some indirect interaction between animals and plants may be taking place at the exclosures. Some frugivorous birds feed on insects when they are nesting (Riehl and Adelson, 2008), and since ant density had increased with time of exclusion (Valenzuela-Galván, data not shown) together with the increase in vegetation cover and structure (de la O-Torres, 2009; Alba-García, 2011; Martínez-Garza, 2010), we hypothesize that generalist birds might be attracted to exclosures to forage not only fruits but also ants, therefore increasing seed rain. Further, attraction of insectivorous

birds that predate arthropods may have positive effects on vegetation cover (Bael et al., 2008), favouring higher animal visitation to plots. However, further studies are needed to clarify these indirect interactions. Cattle exclosures may therefore help reestablish the roles of dispersal agents in this habitat via indirect interaction of birds and arthropods.

4.4. Is natural succession taking place?

Amelioration of harsh abiotic conditions may attract specialist animals which consume and disperse late-successional species from old-growth forest increasing fall of late-successional seeds. Given that recruitment patterns may or not parallel seed rain depending in successional stages of environments (Martínez-Ramos and Sotocastro, 1993; Harms et al., 2000) or microhabitat preferences (Norden et al., 2009), seed rain may be showing natural succession earlier than the recruited community. In Costa Rica, a former pasture was still dominated by wind-dispersed early-successional species from the dry forest *ca.* 7 years after abandonment (Janzen, 1988). The same pattern was also observed in older successional environments originated after heavy agricultural activities and under recurrent perturbation in the dry forest of Western Mexico (Burgos and Maass, 2004). On the other hand, in pastures in Panama a similar percentage of animal and wind-dispersed species were observed in the recruited community after only 3 years of abandoned (Griscom et al., 2009). In this study, 30% of all the seeds recorded within exclosures belonged to three genera of early-successional species dispersed by wind (*Acacia*, *Ipomoea* and *Heliocarpus*) whereas 60% were from the early-successional bird dispersed shrub *H. patens* (Rubiaceae). In the non-excluded plot, *Heliocarpus* spp. comprised 68% of all recorded seeds and any adult of this genus was recorded within this plot. This is the template for recruitment in these early successional environments and the recruitment patterns will depend in the differential colonization capacity of the species. For example, in the advanced regeneration of old gap formations in the rain forest of Los Tuxtlas, Mexico, recruitment of large-seeded local species were favoured over immigrant species falling in low densities (Martínez-Ramos and Sotocastro, 1993) whereas in the mature rain forest of Barro Colorado, Panama, it has been found that the species with higher seed density were recruiting less individuals (negative density-dependence recruitment; Harms et al., 2000). Species dispersed by abiotic vectors (wind or gravity) may had higher colonization capacity (reviewed in Vieira and Scariot, 2006) in this dry forest because of their dispersal timing, physiological requirements and chronic disturbance of vegetation. In the non-excluded plot, the species with the highest seed density was indeed an immigrant species; given that vegetation is still being perturbed at this site, arrival and recruitment of this early successional species dispersed by wind may be favoured for longer time. Within exclosures, a gradual increase in immigrant species dispersed by animals was observed; confirming that succession, at least in terms of potential vegetation is taking place.

Studies of succession with chronosequences have shown that a mature forest structure may be reached after >30 years of succession in abandoned agricultural areas, while species composition may be reached after >80 years if ever (Brown and Lugo, 1990; Kennard, 2002; Ruiz et al., 2005; Lebrija-Trejos et al., 2010). The 30 year old secondary forest studied here shows a tree density (252.5 ind/ha) and basal area (6.18 m²/ha) lower than that reported in the literature for successional dry forests with <8 years of abandonment (Hall and Okali, 1979; Kennard, 2002; Ruiz et al., 2005), albeit with higher annual precipitation than the SHBR (1129–1584 mm vs. 740 mm respectively). In a dry forest with annual precipitation similar to SHBR (Nizanda, Mexico, 900 mm annual precipitation; Lebrija-Trejos et al., 2008), data from a

chronosequence for individuals >5 cm DBH, reveals that basal area of the secondary forest of this study correspond to a successional area of ca. 15 years whereas tree density correspond to a successional areas of ca. 6 years (Lebrija-Trejos, unpublished data). On the other hand, tree density in older forest close to our study area (905 ind/ha, >5 cm DAP; Martínez-Garza, unpublished data) showed slightly lower values to those reported in mature dry forests with higher annual rainfall (ca. 1000 ind/ha; Kennard, 2002) and much lower to mature dry forest with similar annual rainfall (2125 ind/ha; Lebrija-Trejos, unpublished data). Is this disparity in successional trajectory due to the chronic perturbation caused by cattle? The increase in potential vegetation richness and density measured as seed rain within exclusions with time and also compared to a non-excluded site indicates that this may be indeed the case.

4.5. Implications for forest management and restoration

Vegetation dynamics in secondary tropical dry forest under frequent perturbation by cattle have been largely ignored (but see, Blackmore and Vitousek, 2000; Stern et al., 2002), even though such forests cover large areas. Secondary forest used show higher diversity than man-made pastures denuded of all native tree diversity and may be reservoirs of high tree diversity (Chazdon et al., 2009). However, when these forests are used for cattle ranching activities, grazing by cattle directly affect plants, but also disturb fauna and the interactions of animals and plants. When forest is protected, birds and bats visit these protected areas even when wind-dispersed tree species dominate standing vegetation.

The evidence that the phenologies of seed rain dispersed by biotic and abiotic factors at successional dry environments seem to be exceptionally constant across years suggests that most seeds (mainly from wind-dispersed species) adjust to spending ca. 4 months in the soil, before the onset of rain and germination, whereas species falling during the rainy season should germinate immediately or be exposed to predation and desiccation for ca. 1 year. This regular annual phenology may allow managers and restorationist to plan for the best time to collect the highest number of species to propagate them; this also will allow, as suggested by Vieira et al. (2008), to collect seeds from many species and use them for direct seeding once rainy season is well established. Wind-dispersed species seem to buffer the negative effects of predation and desiccation while in the seed bank by dispersing an immense amount of seeds. However, late-successional, wind-dispersed species with large seeds (*Swietenia macrophylla*, Gutierrez-Granados et al., 2011), may never arrive to these early successional areas. Late-successional animal- and wind-dispersed species should be planted or introduced by direct seeding during the rainy season to increase richness in species-poor secondary forests.

Studies in frequently perturbed secondary dry tropical forest report the dominance of abiotically dispersed *Acacia* spp. and *Mimosa* spp. in the established community (Miller and Kauffman, 1998; Roth, 1999; Lebrija-Trejos et al., 2008), and these species may prohibit succession in some forests (Burgos and Maass, 2004). In this study, two *Acacia* and one *Mimosa* spp. accounted for 22% of the seeds recorded in the seed rain and were two of the species which dominated the standing vegetation (54% of trees ≥ 5 cm DBH,

Table A1

Tree species, dispersal mode (biotic [birds and bats], abiotic [wind or gravity], stem density (trees ha⁻¹) and basal area (m² ha⁻¹) of woody individuals of ≥ 5 cm DBH within eight exclosures of secondary dry tropical forest in Sierra de Huautla, Morelos, Mexico. Species are arranged by density.

Species ^a	Family	Dispersal mode	Density	Basal area
<i>Acacia cochliacantha</i> Humb. & Bonpl. ex Willd.	Fabaceae	Abiotic ^b	75.50	1.100
<i>Ipomoea pauciflora</i> Mart. & Gal.	Convolvulaceae	Abiotic	49.00	2.000
<i>Mimosa benthamii</i> McBride	Fabaceae	Abiotic	31.50	0.550
<i>Sapium macrocarpum</i> Muell. Arg.	Euphorbiaceae	Biotic	13.00	0.330
<i>Acacia farnesiana</i> Willd.	Fabaceae	Abiotic ^b	12.00	0.060
<i>Heliocarpus</i> sp.	Tiliaceae	Abiotic	8.00	0.290
<i>Ruprechtia fusca</i> Fernald	Polygonaceae	Abiotic	8.00	0.085
<i>Lysiloma divaricatum</i> Macbride	Fabaceae	Abiotic	7.50	0.180
<i>Bursera copallifera</i> (Sessé & Moc. Ex DC.) Bullock	Burseraceae	Biotic	6.50	0.260
<i>Ceiba aesculifolia</i> (h. B. & K.) Britten & E.G. Baker	Bombacaceae	Abiotic	5.00	0.240
<i>Conzattia multiflora</i> Standley	Fabaceae	Abiotic	5.00	0.160
<i>Acacia coulteri</i> Benth. Ex A. Gray	Fabaceae	Abiotic	3.50	0.050
<i>Bursera aloexylon</i> Engl.	Burseraceae	Biotic	3.00	0.085
<i>Euphorbia schlechtendalii</i> Boiss.	Euphorbiaceae	Biotic	3.00	0.016
<i>Malpighia mexicana</i> A. Juss.	Malpighiaceae	Biotic	2.50	0.120
<i>Lysiloma acapulcense</i> Benth.	Fabaceae	Abiotic	2.00	0.110
<i>Spondias purpurea</i> Linn.	Anacardiaceae	Biotic	2.00	0.110
<i>Vitex mollis</i> H.B. & K.	Verbenaceae	Biotic	2.00	0.075
<i>Vitex pyramidata</i> Robinson & Pringle	Verbenaceae	Biotic	2.00	0.014
<i>Lochocarpus</i> sp.	Fabaceae	Abiotic	1.50	0.024
<i>Trichilia hirta</i> Linn.	Meliaceae	Biotic	1.50	0.022
<i>Amphipterygium adstringens</i> (Schlechtend.) Schiede ex Standley	Julianaceae	Abiotic	1.00	0.020
<i>Bunchosia canescens</i> DC.	Malpighiaceae	Biotic	1.00	0.020
<i>Bursera bicolor</i> Engl.	Burseraceae	Biotic	1.00	0.017
<i>Bursera lancifolia</i> Engl.	Burseraceae	Biotic	1.00	0.003
<i>Randia echinocarpa</i> (Moc. & Sessé) ex DC.	Rubiaceae	Biotic	1.00	0.002
<i>Bursera grandifolia</i> Engl.	Burseraceae	Biotic	0.50	0.060
<i>Ipomoea murucoides</i> Roem. & Schult.	Convolvulaceae	Abiotic	0.50	0.030
<i>Leucaena</i> sp.	Fabaceae	Abiotic	0.50	0.020
<i>Mimosa polyantha</i> Benth.	Fabaceae	Abiotic	0.50	0.010
<i>Pseudosmodium perniciosum</i> Engl.	Anacardiaceae	Abiotic	0.50	0.002
<i>Stemmadenia bella</i> Miers	Apocynaceae	Biotic	0.50	0.001
<i>Thevetia thevetioides</i> Schum.	Apocynaceae	Biotic	0.50	0.001

^a Nomenclature follows Dorado et al. (2005a).

^b Potentially dispersed by livestock (reviewed in Miceli-Méndez et al., 2008).

Table A2

Diet, functional group and abundance of ant genera recorded in March 2006 within eight exclosures of secondary dry tropical forest, Sierra de Huautla, Morelos, Mexico.

Genera	Diet ^a	Functional group ^b	Abundance
<i>Atta</i> sp.	Leaf cutter and Fungivore	Attini	204
<i>Camponotus</i> (4 spp.)	Honeydew, nectar/Omnivore	Subordinate Camponitini	45
<i>Crematogaster</i> sp.	Omnivore	Generalized Myrmicine	2
<i>Dorymyrmex</i> sp.	Opportunistic omnivore	Opportunist/Dominant Dolichoderinae	19
<i>Forelius</i> (2 spp.)	Omnivore	Dominant Dolichoderinae	46
<i>Leptothorax</i> sp.	Omnivore	Cryptic species	11
<i>Monomorium</i> sp.	Seed harvester/Omnivore	Generalized Myrmicine	29
<i>Odontomachus</i> sp.	Predator	Specialized predator	2
<i>Pheidole</i> (2 spp.)	Scavenger/predator/seed harvester	Generalized Myrmicine	1769
<i>Pogonomyrmex</i> sp.	Seed harvester	Hot Climate Specialist	1337
<i>Solenopsis</i> sp.	Seed harvester/Omnivore	Tropical Climate Specialist	105
<i>Tetramorium</i> sp.	Omnivore	Opportunist	3

^a Diet based in Hölldobler and Wilson (1990) and Weiser and Kaspari (2006).^b Functional groups based on Bestelmeyer and Wiens (1996) and Andersen (1997).**Table A3**Bird species, family, abundance (Abun), substrate where regularly observed (C = canopy, M = middle [brushes, barks, pasture], G = ground), diet (I = insectivore, F = frugivore, Gr = granivore, O = omnivore [insects, fruit, small vertebrates]) in June–August 2007 within six exclosures of secondary dry tropical forest in Sierra de Huautla, Morelos, Mexico.^a

Species	Family	Abun	Substrate	Diet ^b
<i>Columbina inca</i>	Columbidae	61	G–M	Gr
<i>Centurus hypopolius</i>	Picidae	16	C	F, I
<i>Icterus wagleri</i>	Emberizidae	4	C	F, I
<i>Myiodynastes luteiventris</i>	Tyrannidae	22	C	I, F
<i>Passerina versicolor</i>	Emberizidae	20	M	I
<i>Icterus pustulatus</i>	Emberizidae	42	C	F, I
<i>Turdus rufopalliat</i>	Muscicapidae	17	C	I
<i>Myarchus tyrannus</i>	Tyrannidae	14	C	I, F
<i>Aimophila humeralis</i>	Emberizidae	22	G–M	Gr, I
<i>Picoides scalaris</i>	Picidae	5	C	F, I
<i>Pheucticus chrysopleus</i>	Emberizidae	18	C	F
<i>Aimophila ruficauda</i>	Emberizidae	50	G–M	Gr, I
<i>Molothrus aeneus</i>	Emberizidae	16	C	O
<i>Centurus chrysogenys</i>	Picidae	12	C	F, I
<i>Coccyzus minor</i>	Cuculidae	2	C	I
<i>Xenotriccus mexicanus</i>	Tyrannidae	2	C	I
<i>Passerina leclancherii</i>	Emberizidae	4	M	I
<i>Momotus mexicanus</i>	Momotidae	2	C	F, O
<i>Trogon mexicanus</i>	Trogonidae	7	C	F, I
<i>Vireo hypochryseus</i>	Vireonidae	1	M–C	I
<i>Tyrannus melancholicus</i>	Tyrannidae	2	C	F, I
<i>Quiscalus mexicanus</i>	Emberizidae	1	C	O
<i>Dendroica coronata</i>	Emberizidae	2	M	F, I
<i>Columbina minuta</i>	Columbidae	9	G–M	Gr, I
<i>Euphonia elegantissima</i>	Emberizidae	3	M–C	F
<i>Leptotila verreauxi</i>	Columbidae	2	G	Gr
<i>Sporophila torqueola</i>	Emberizidae	1	G–M	Gr
<i>Piranga ludoviciana</i>	Emberizidae	3	M–C	F, I
<i>Empidonax traillii</i>	Tyrannidae	2	C	I
<i>Ptyrocephalus rubinus</i>	Tyrannidae	3	C	I
<i>Troxostoma curvirostre</i>	Mimidae	4	M	F

^a Bird were registered within plots from counting points, recording them in a particular radio of distance (from the point) and using reference markers. In each census we checked resident, nesting and leking birds and we did not count double birds returning at their nest or territorial perch, or site. We avoid counting birds twice by maintaining a mental note of bird movements inside the plot (following suggestion from Bibby et al., 2000).^b Diet based on Howell and Webb (1995), Sigala (2009), pers. obs.

Appendix Table A1). These species seem to be favored by perturbation, but it remains to be shown whether after longer time spans, they will still dominate at sites excluded from anthropogenic perturbation that only experience natural disturbance (i.e., fall of branches and trees). Gradual change in composition towards higher percentage of animal dispersed species and further increases in biodiversity to later successional stages may take place as predicted by seed rain, but at an extremely slow pace. To increase bio-

diversity and speed the natural process of succession in excluded areas, late-successional species should be planted (Martínez-Garza and Howe, 2003) or seeded (Cole et al., 2011). Excluded areas may serve as islands of biodiversity for the movement of metapopulations of native animals and plants (Vandermeer and Carvajal, 2001) and source gardens (sensu Suding and Gross, 2006) while non-excluded areas may remain productive for cattle grazing and wood extraction activities.

5. Conclusions

In poor-species dry forests, monitoring of changes in composition of the seed rain by the dispersal mode, successional status of species and in comparison with standing tree community are more relevant than richness and seed density alone to detect natural succession with time of exclusion. The monthly pattern of seed rain at this successional dry environment is extremely regular in time, as predicted, allowing managers to easily plan for collecting species for propagation and direct seeding. Early-successional species dominate the seed rain community after 3 years of exclusion contrary to expectations; however 70% of immigrant species falling within plots were late-successional species and a high percentage of immigrant species dispersed by animals is noted with time of exclusion and in comparison to the seed rain falling at the non-excluded plot. To speed up the recovery of biodiversity and the natural process of succession in these areas, late-successional species should be planted or seeded.

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Appendix A

See Appendix Tables A1–A4.

Table A4

Species and density of seeds (m²/month) and the average for three years in the seed rain within eight exclosures and at one non-excluded site over 4 months (January–April, 2010) in a secondary dry forest at Sierra de Huautla, Morelos, Mexico. Indicated are family, dispersal mode (Disp; Abiotic [wind and gravity] and Biotic [animals]) and successional status (Succ s; Early-successional and Late-Successional). Numbers following dispersal mode or successional status indicate reference to those attributes for the species, attributes with no references are personal observations.

Species	Family	Disp	Life form ^a	Succ s	Density of seeds				
					Exclosure				Non-excluded
					Y 1	Y 2	Y3	Average	4 months
<i>Acacia cochliacantha</i> Humb. & Bonpl. ex Willd.	Fabaceae	Abiotic ^b	S	Early ^{c,d}	8.91	7.08	10.33	8.77	1.79
<i>Acacia farnesiana</i> (L.) Willd.	Fabaceae	Abiotic ^{b,e}	S	Early ^{d,e}	0.30	0.26	0.13	0.23	
<i>Amphipterygium adstringens</i> (Schltdl.) Standl.	Julianaceae	Abiotic ^f	T	Late ^c	0.02	0.68	0.01	0.24	0.24
<i>Astianthus viminalis</i> (Kunth) Baill.	Bignoniaceae	Abiotic ^g	T	Late	–	0.01	<0.01	<0.01	
<i>Bunchosia canescens</i> (W.T. Aiton) DC.	Malpighiaceae	Biotic ^o	S	Early	–	–	<0.01	<0.01	
<i>Bursera bicolor</i> (Willd.) Engl.	Burseraceae	Biotic	T	Late	0.17	0.11	0.09	0.13	
<i>Bursera copallifera</i> (DC.) Bullock	Burseraceae	Biotic	T	Late	0.16	0.41	0.18	0.25	
<i>Bursera glabrifolia</i> (Kunth) Engl.	Burseraceae	Biotic	T	Late	0.04	0.03	0.01	0.03	
<i>Bursera grandifolia</i> (Schltdl.) Engl.	Burseraceae	Biotic	T	Late	0.01	0.01	0.01	0.01	
<i>Bursera lancifolia</i> (Schltdl.) Engl.	Burseraceae	Biotic ^h	T	Late	0.26	0.39	0.27	0.31	
<i>Cedrela oaxacensis</i> C. DC. & Rose	Meliaceae	Abiotic	T	Late	–	–	<0.01	<0.01	
<i>Ceiba parvifolia</i> Rose	Bombacaceae	Abiotic	T	Late	0.02	0.07	–	0.03	0.03
<i>Celtis caudata</i> Planch.	Ulmaceae	Biotic ⁱ	T	Early ^c	–	<0.01	<0.01	<0.01	
<i>Cissus sicyoides</i> L.	Vitaceae	Biotic	Wv	Early	0.16	0.78	0.75	0.56	0.03
<i>Clematis dioica</i> L.	Ranunculaceae	Abiotic	Wv	Early ^j	0.01	0.02	0.02	0.02	
<i>Conzattia multiflora</i> (B.L. Rob.) Standl.	Fabaceae	Abiotic ^k	T	Late	<0.01	0.01	0.03	0.01	0.05
<i>Cordia morelosana</i> Standl.	Bignoniaceae	Abiotic	T	Late	–	–	0.02	<0.01	
<i>Crataeva palmeri</i> Rose	Capparaceae	Biotic	T	Late	<0.01	<0.01	–	<0.01	
<i>Crescentia alata</i> Kunth	Bignoniaceae	Abiotic	T	Late	0.13	0.01	–	0.05	
<i>Eysenhardtia polystachya</i> (Ortega) Sarg.	Fabaceae	Abiotic	T	Early ^d	–	0.01	–	<0.01	
<i>Ficus cotinifolia</i> Kunth	Moraceae	Biotic ^b	T	Late	0.18	0.02	<0.01	0.08	
<i>Ficus</i> sp. 1	Moraceae	Biotic ^l	T	Late	0.08	0.16	0.88	0.37	
<i>Ficus</i> sp. 2	Moraceae	Biotic ^l	T	Late	0.07	<0.01	–	0.03	
<i>Ficus</i> sp. 3	Moraceae	Biotic ^l	T	Late	0.08	<0.01	0.06	0.05	
<i>Ficus</i> sp. 4	Moraceae	Biotic ^l	T	Late	–	0.11	0.20	0.10	
<i>Ficus</i> sp. 5	Moraceae	Biotic ^l	T	Late	–	<0.01	<0.01	<0.01	
<i>Ficus</i> sp. 6	Moraceae	Biotic ^l	T	Late	–	<0.01	–	<0.01	
<i>Ficus</i> sp. 7	Moraceae	Biotic ^l	T	Late	–	–	0.11	0.04	
<i>Ficus</i> sp. 8	Moraceae	Biotic ^l	T	Late	–	–	0.02	0.01	
<i>Gaudichaudia alba</i> Schltdl. & Cham.	Malpighiaceae	Abiotic	Wv	Early	0.02	0.07	0.73	0.27	
<i>Guazuma ulmifolia</i> Lam.	Sterculiaceae	Biotic ^f	T	Early ^f	0.42	0.19	0.09	0.23	
<i>Hamelia patens</i> Jacq.	Rubiaceae	Biotic ^o	S	Early ^o	16.8	66.37	34.94	39.37	8.70
<i>Heliocarpus</i> sp.	Tiliaceae	Abiotic	T	Early	12.19	12.36	3.18	9.24	41.27
<i>Indigofera cuernavacana</i> Rose	Fabaceae	Abiotic	S	Early	–	–	<0.01	<0.01	
<i>Ipomoea pauciflora</i> Mart. & Gal.	Convolvulaceae	Abiotic ^b	T	Early	1.50	1.36	1.57	1.48	1.08
<i>Ipomoea murucoides</i> Roem. & Schult.	Convolvulaceae	Abiotic ^b	T	Early	–	0	0.12	0.09	
<i>Lantana camara</i> L.	Verbenaceae	Biotic ^m	S	Early ^c	–	<0.01	0.18	0.06	
<i>Leucaena esculenta</i> (Moc. & Sessé ex DC.) Benth.	Fabaceae	Abiotic ^d	T	Early ^d	–	–	0.01	<0.01	
<i>Lonchocarpus</i> sp.	Fabaceae	Abiotic ^k	T	Late	0.01	0.02	–	0.01	
<i>Lysiloma acapulcense</i> (Kunth) Benth.	Fabaceae	Abiotic ^d	T	Late ^d	–	–	<0.01	<0.01	
<i>Lysiloma divaricatum</i> (Jacq.) J.F. Macbr.	Fabaceae	Abiotic ^{b,d}	T	Late ⁿ	0.05	1.11	0.01	0.39	6.46
<i>Malpighia mexicana</i> A Juss	Malpighiaceae	Biotic	T	Late	–	<0.01	0.09	0.03	
<i>Marsdenia zimapanica</i> Hemsf.	Asclepiadaceae	Abiotic ^p	Wv	Early ^p	0.02	0.08	0.04	0.05	0.03
<i>Mascagnia polybotrya</i> Nied.	Malpighiaceae	Abiotic	Wv	Early	0.99	0.86	0.99	0.95	0.08
<i>Matelea trachyantha</i> (Greenman) W.D. Stevens	Apocynaceae	Abiotic ^p	S	Early	–	0.02	–	<0.01	
<i>Mimosa alba</i> Hum. & Bonpl. ex Willd.	Fabaceae	Abiotic	S	Early ^k	–	–	<0.01	<0.01	
<i>Mimosa benthamii</i> J. F. Macbr.	Fabaceae	Abiotic ^d	T	Early ^{d,k}	0.04	1.33	0.08	0.48	0.45
<i>Mimosa polyantha</i> Benth.	Fabaceae	Abiotic ^d	S	Early ^{d,k}	–	–	<0.01	<0.01	
<i>Nissolia fruticosa</i> Jacq.	Fabaceae	Abiotic ^k	Wv	Early ^k	0.21	0.14	0.49	0.28	0.05
<i>Opuntia puberula</i> Pfeiff.	Cactaceae	Biotic	S	Early	0.02	0.04	<0.01	0.02	
<i>Pachycereus grandis</i> Rose	Cactaceae	Biotic ^o	T	Late	0.34	0.56	0.17	0.36	
<i>Pithecoctenium crucigerum</i> (L.) A. H. Gentry	Bignoniaceae	Abiotic ^g	Wv	Early	0.02	0.02	0.01	0.01	
<i>Pseudosmodium perniciosum</i> (Kunth) Engl.	Anacardiaceae	Abiotic ^b	T	Early	<0.01	0.02	<0.01	<0.01	
<i>Randia echinocarpa</i> Moc. & Sessé	Rubiaceae	Biotic	S	Early	–	0.01	–	<0.01	0.05
<i>Ruprechtia fusca</i> Fernald.	Polygonaceae	Abiotic ^f	T	Late	–	–	0.20	0.07	
<i>Sapium macrocarpum</i> Müll. Arg.	Euphorbiaceae	Biotic	T	Late	0.10	0.33	0.10	0.18	
<i>Serjania</i> sp.	Sapindaceae	Abiotic	Wv	Early	0.04	0.01	0.02	0.03	
<i>Thevetia thevetioides</i> (Kunth) K. Schum.	Apocynaceae	Biotic ^b	T	Late	–	–	<0.01	<0.01	
<i>Trichilia hirta</i> L.	Meliaceae	Biotic	T	Early ^j	<0.01	0.02	0.01	0.01	
<i>Verbesina</i> sp.	Asteraceae	Abiotic	Wv	Early	0.85	1.65	0.84	1.11	0.03
<i>Vitex mollis</i> H.B. & K.	Verbenaceae	Biotic ^m	T	Late	0.01	–	0.01	0.01	

^a Life form: T = tree, S = shrub, Wv = woody vine.

^b Ceccon and Hernández (2009).

^c Salas et al. (2007).

^d Cervantes et al. (2001).

^e Vázquez et al. (1999).

^f Pennington and Sarukhán (2005).

^g Gentry (1982).

^h Rzedowski et al. (1992).

- ⁱ Nee (1984).
- ^j Castillo et al. (2007).
- ^k Dorado et al. (2005b).
- ^l Piedra-Malagón et al. (2006).
- ^m Willmann et al. (2000).
- ⁿ Castro Luna (2007).
- ^o Sigala-Rodríguez (2009).
- ^p Juárez-Jaimes and Lozada (2010).
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