

Early recruitment dynamics in tropical restoration

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Abstract. Unassisted secondary succession in abandoned tropical pastures often results in species-poor forests of pioneer trees that persist for decades. We characterize recruitment rates of woody vegetation in planting treatments during the first 60 months of experimental restoration on thin, eroded soils at Los Tuxtlas, southern Mexico. We test the hypothesis that recruitment of later-successional trees is greater in fenced plots planted with native trees than in fenced controls that simulate natural succession, and further that recruitment of such species would be greater in plots planted with animal-dispersed trees than in those planted with wind-dispersed trees.

Results indicated much greater recruitment of later-successional animal-dispersed trees in planted plots as compared with controls. Three censuses per year recorded 960 recruited individuals of 44 species of trees and shrubs from 20–60 months after cattle exclusion. Ninety-six percent of recruits were not of planted species. Repeated-measures analyses of variance indicated that recruited communities included more species of pioneers than of later-successional trees and shrubs, with more individuals and species dispersed by animals than by wind. Recruitment of pioneers did not differ between control and planted plots. Later-successional recruits dispersed by animals accumulated >10 times faster in planted than control plots, with apparent acceleration after planted *Cecropia obtusifolia* and *Ficus yoponensis* first produced fleshy fruits 48 months after cattle exclusion. Sparse later-successional wind-dispersed recruits did not differ by treatment. Our preliminary results over the first five years after cattle exclusion indicate that planted stands clearly accelerate succession through accumulation of later-successional trees and shrubs dispersed by animals.

Key words: dispersal mode; experimental restoration; life history; Mexico; movement ecology; seed dispersal; seedling establishment; succession; tropical rainforest.

INTRODUCTION

The relationship between deforestation and forest regeneration will determine the future of tropical biomes. Tropical forests have the highest biodiversity of all terrestrial ecosystems (Turner 1996, Dirzo 2001), yet total deforestation and forest fragmentation are rapidly destroying much of the remaining old-growth forest between the Tropic of Capricorn and the Tropic of Cancer (Houghton 1994, Ojima et al. 1994, Bryant et al. 1997, Fahrig 2003, Fearnside 2005). Less appreciated is the rapid growth of secondary forest on land that has been abandoned (Chazdon 2003, Rudel et al. 2005, Wright 2010). Assisted regeneration and full-scale forest restoration have potentially important roles in regaining lost biodiversity and ecosystem services. A challenge, addressed here, is to test means of accelerating revegetation of patches to connect forest fragments in permanent agricultural mosaics where substantial land

area will not be abandoned to natural succession or set aside for ecological restoration.

Natural succession occurs at different rates under different circumstances. Succession is slower in abandoned pasture than on land with histories of subsistence agriculture, or logged areas that are allowed to recover without further disturbance (Aide et al. 1995). High-intensity, long-term cattle ranching slows ecosystem capacity to recover biodiversity (Uhl et al. 1988, Nepstad et al. 1991, Jones et al. 2003, Myster 2004, Benítez-Malvido and Lemus-Albor 2005). Depleted seed banks, compacted soil, depleted soil nutrients, intense solar radiation, low seed input, and high rates of seed and seedling predation limit recolonization and growth by late-successional forest trees. Pastures under continued cattle grazing do not regenerate forest.

The rate of recovery of forest richness in abandoned pasture is influenced by dispersal mode and life history of colonizing plants. Small seeds carried long distances by wind, often of a few ubiquitous species, arrive unassisted in disturbed areas (Janzen 1988, Ingle 2003, Howe et al. 2010). A paradox and a challenge for recovery of tropical diversity on badly degraded land is that the great majority of tropical rain forest trees and

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shrubs are dispersed by animals (e.g., Frankie et al. 1974, Howe and Smallwood 1982, Wang and Smith 2002), yet many birds and mammals of the forest interior avoid crossing open areas, or require unusual motivation to do so. Most animal-dispersed seeds of forest interior do not arrive in extensive pastures until their dispersal agents seek cover or food in isolated trees or small stands of trees (Estrada and Coates-Estrada 2001, 2005). A generalization across the tropics seems to be that large open areas of grasses on thin, eroded soils are slow to recover by unassisted succession because of severe dispersal limitation and adverse conditions for seeds and germinating seedlings.

Here we report seedling establishment by life history and dispersal mode in pasture plots for the first five years of an experiment expected to last 30 years. We hypothesize that mixed plantings of native trees accelerate assisted compared to natural succession (reviewed in Martínez-Garza and Howe 2003). In early stages of succession, planted early successional species (fruiting pioneers as contrasted with later-successional species; see *Methods*) accelerate recruitment of primary-forest species that may not otherwise establish in pasture for years to decades. One compelling question is whether these plantings shape the structure of the recruited communities more than would occur by unassisted succession. Another question, to be addressed as our experimental plantings mature, is whether recruitment differs in different kinds of plantings.

We test the effects of planting treatments, life-history, and dispersal mode on recruitment rates in the first 60 months after cattle exclusion. We expect an overall increase of recruitment rates, especially for pioneer species with small mobile seeds. We hypothesize that recruitment by animal-dispersed species will be higher under plantings than in fenced but unplanted plots that simulate natural succession. We further hypothesize that wind-dispersed recruits will not show distinctive recruitment patterns based on treatments prior to maturation of planted species. Ultimately, as numerous experimental animal-dispersed trees mature and provide food for wide-ranging animals that eat fruit and disperse seeds, we expect dramatically higher recruitment of forest species in plantings of animal-dispersed than plantings of wind-dispersed trees. The surprise at five years is that individual recruitment of later-successional trees dispersed by animals is much higher in planted plots than is recruitment of pioneers in any treatment; even sparse, non-reproductive tree plantings play an important role in re-establishing biodiversity of later-successional trees.

METHODS

Study area and species

This study was conducted at Los Tuxtlas, Veracruz, Mexico (18°05'18 N and 18°45' N; 94°35' W and 95°30' W). The Los Tuxtlas forest is 3300 km² in area and ranges in elevation from 200 to 1700 m above sea level (Dirzo et al. 1997). This volcanic region is characterized

by acidic soils (pH 4.9) with a large clay component (48.5% clay), having formed from basaltic and andesitic rock mixed with volcanic ash (see Guevara et al. 2004). Records of the Los Tuxtlas Biological Station of the Universidad Nacional Autónoma de México show mean annual precipitation of 4825 mm per year from 1997 to 2006 (Martínez-Garza et al. 2011), a rainy season from June to February and a dry season from March to May, and a mean annual temperature of 25°C (see Soto and Gama 1997). The formerly forested land in which our plots were established has been under intensive cattle ranching for at least 30 years on ground planted with native (*Axonopus compressus* and *Paspalum conjugatum*) and exotic (*Cynodon dactylon*, *Brachiaria brizantha*, *Brachiaria decumbens*, and *Panicum* spp.) grasses. Soil depth ranges from 5 to 72 cm over volcanic rock, with a mean depth of 26.8 ± 14.2 cm (mean ± SD) (Howe et al. 2010, Tobón et al. 2011). Nearby forest holds ~300 native tree species (Ibarra-Manríquez and Sinaca 1995, 1996a, b). In Los Tuxtlas landscapes, 81% of 364 sampled plant species occur in fragments <5 ha; 58% of species in small fragments in even the most highly fragmented areas are old-growth trees (Arroyo-Rodríguez et al. 2008). More than 150 fruit-eating birds and mammals occupy the Los Tuxtlas landscape (Estrada et al. 1993), with wide-ranging fruit-eating bats (e.g., *Artibeus* spp., *Sturnira* spp.) and birds (*Dryocopus lineatus*, *Gymnostinops montezuma*, *Psilorhinus morio*, *Ramphastos sulfuratus*) among the most likely dispersal agents of seeds arriving in our developing planted stands (H. F. Howe, *unpublished data*).

Planted and recruited species were classified as pioneer or later successional, and as animal dispersed or wind dispersed. Life-history designations are problematic where authors place the same species in different categories and use several categories (pioneer vs. persistent; early pioneer, late pioneer, vs. late successional; pioneer vs. old-growth; generalist vs. specialist; e.g., Martínez-Ramos 1985, Purata 1986, Ibarra-Manríquez and Oyama 1992, Arroyo-Rodríguez et al. 2008, Chazdon et al. 2011). Because the data at hand do not lend themselves to statistical distinctions of pasture recruits into several categories (cf. Chazdon et al. 2011 for secondary and primary forests), we use demographic and associational analyses from the Los Tuxtlas region to categorize species as “pioneers” common in early succession and other “later-successionals” (e.g., Purata 1986, Ibarra-Manríquez and Oyama 1992). This parallels the distinction by Arroyo-Rodríguez et al. (2008) and Howe et al. (2010) between pioneer and old-growth species.

Distinction of animal- and wind-dispersed species is straightforward. Animal-dispersed species are those with fleshy fruits with pulp surrounding seeds as drupes, berries, pomes, dehiscent capsules or indehiscent pods, as compared with wind-dispersed seeds with wings, balloons, plumes, or other structures that greatly increase surface-to-volume ratios (e.g., Howe and

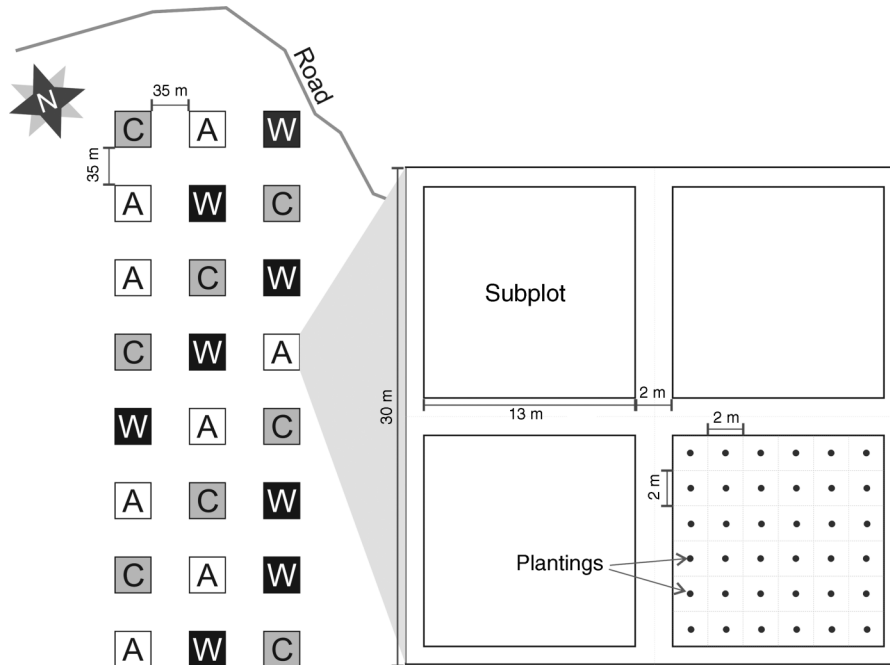


FIG. 1. Experimental design of fenced plots. Illustrated are plantings of 12 animal-dispersed species (A), 12 wind-dispersed species (W), and unplanted controls (C).

Smallwood 1982, van der Pijl 1982). Species with fruit structures consistent with water dispersal, ballistic dispersal, or hard nuts hoarded by rodents or dispersed by gravity are not present in the sample. Seeds are often re-dispersed by secondary agents, but rodents likely to carry seeds substantial distances (e.g., the agouti, *Dasyprocta mexicana*) are not present in the plots.

Experiment

In June 2006, we established 24 cattle exclusion plots arrayed in a 3×8 grid in 12 ha of active pasture with a slope from 180 to 260 m above sea level. Remnant trees were removed during site preparation. Each 30×30 m plot was subdivided into four 13×13 m subplots available for seedling establishment, with 2 m crossed central aisles clear of woody vegetation and 1 m external edge cleared by cattle reaching through fences (Fig. 1). Plots were defined with three-strand fences of barbed wire fastened to living poles of *Gliricidia sepium* (Fabaceae), a gravity-dispersed tree that was trimmed regularly to prevent fruiting. Initial planting was between June and December 2006. Plots were replanted in September and October 2007 after an extended seasonal drought killed the first cohorts (Martínez-Garza et al. 2011). Eight exclosures were planted with 12 animal-dispersed species (four pioneer and eight later-successional tree species); another eight exclosures were planted with 12 wind-dispersed species (four pioneers and eight later-successional tree species; Appendix A). Eight unplanted exclosures served as controls. Each subplot was planted in a 6×6 grid, with a total per plot of 144 plants (12 of

each of 12 species) separated by 2 m from each other (Fig. 1). Twelve species in 16 planted plots were spaced to maximize distance between conspecifics within each subplot. Growing vegetation within 50 cm of planted seedlings was removed monthly until the sapling was taller than surrounding grass (to 1.5 m high). The matrix between fenced plots remained short, closely cropped grass in active pastures that were maintained as part of the experimental design. Cattle consumed seedlings and kept grasses cropped up to 1 m inside fences.

Plots differed in distance to forest. Plot midpoints were 90–480 m from 30–40-year-old secondary forest (241 ± 18 m [mean \pm SE]) to the south and southeast of the grid, and 236–409 m from privately owned primary forest to the east (324 ± 12 m). Taller old-growth forest of the Los Tuxtlas Biological Station was 344–800 m (568 ± 31 m) to the south of plots.

Woody seedlings >10 cm high, excluding planted individuals, were counted in each fenced plot every four months from 20 through 60 months after cattle exclusion. Recruited species were identified, tagged, and measured (height and basal diameter, with diameter at breast height and canopy width for growing trees). Re-sprouts of pre-existing trees (0–3 per plot) were cut. These were not counted in censuses. Nomenclature followed Ibarra-Manriquez and Sinaca (1995, 1996a, b; see Appendices A and B).

Statistical analyses

The basic tool of the following analyses is repeated-measures ANOVA. We use a factorial design in which

samples of recruits are measured every four months, where the number of months since cattle exclusion is the repeated factor. Dependent variables are species recruitment rate for the first repeated-measures ANOVA, recruitment rate regardless of species for the second (hereafter “individual recruitment”). The repeated-measures ANOVAs included planting treatment with three levels (plots planted with animal-dispersed species, planted with wind-dispersed species, and unplanted controls); life history with two levels (pioneer and later-successional recruits); and dispersal mode with two levels (recruits from seeds dispersed by animals or wind). We evaluated overall significance levels for repeated measures using the Greenhouse-Geisser correction for sphericity. Means are accompanied by standard deviations unless otherwise indicated.

Statistical analyses were performed using STATISTICAL CA 7.0 (StatSoft, Tulsa, Oklahoma, USA) and SYSTAT 13 (Chicago, Illinois, USA). Derivative estimates and metrics addressing community structure (projected richness, alpha and beta diversities, multidimensional scaling, and similarity indices) will be developed elsewhere.

RESULTS

Overview

During 60 months of cattle exclusion, 44 woody species from 27 families recruited in a density of 0.057 individuals/m² (Appendix B). Overall survival of recruits was 81% after 60 months of cattle exclusion. Common families included Melastomataceae, Euphorbiaceae, and Piperaceae, with four, four, and three species, respectively. *Bursera simaruba* (Burseraceae), a later-successional animal-dispersed tree that is widely used as a shade tree and in living fences, had the highest density (0.017 individuals/m²). *Cordia alliodora* (Boraginaceae), a pioneer species dispersed by wind, and *Conostegia xalapensis* (Melastomataceae), a pioneer animal-dispersed shrub, were the second and third most important species by density (0.008 and 0.004 individuals/m², respectively). Fifty-six percent of the recruited seedlings were pioneers, 67% of which were of animal-dispersed taxa. The remaining 44% of the seedlings were later-successionals, of which 87% were animal dispersed and 13% wind dispersed.

Between 20 and 60 months since cattle exclusion, repeated-measures ANOVA indicated increases in recruitment of species and individuals. Species recruitment rate increased significantly over time in a roughly linear fashion ($F_{10, 840} = 51.11$, $P < 0.00001$; Fig. 2a). Individual recruitment also increased, with apparent acceleration between 44 and 60 months (repeated-measures $F_{10, 840} = 21.72$, $P < 0.00001$; Fig. 2b). Of most interest were within-subject interactions of main effects with time.

Interactions with time

Interactions of time and response variables were evident. Interaction between time and planting treat-

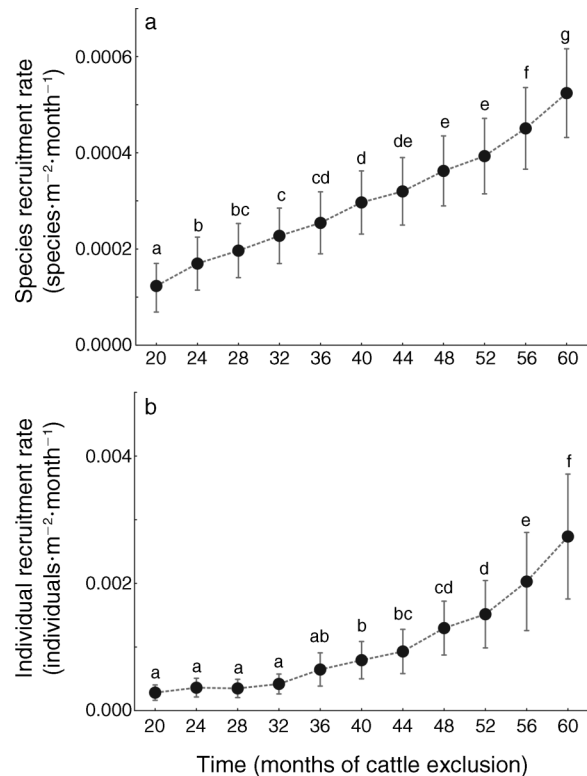


FIG. 2. Species and individual recruitment rates through 60 months of cattle exclusion (through June 2011) for (a) species and (b) individuals. Shown are means with 95% confidence intervals. Note differences in scales of y-axes. Different letters indicate significant differences between time periods based on post-hoc Tukey tests at $P < 0.05$.

ments from 20 through 60 months showed significantly higher recruitment rates in planted vs. control plots for species (repeated-measures $F_{20, 840} = 2.54$, $P = 0.0002$; Fig. 3a) and individuals ($F_{20, 840} = 3.33$, $P < 0.0001$; Fig. 3b). Interaction of time and life history showed a significantly higher increase of pioneer species recruitment rate as compared with later-successional species (repeated-measures $F_{10, 840} = 11.43$, $P < 0.0001$; Fig. 4a). Individual recruitment rates did not differ by life histories ($F_{10, 840} = 0.95$, $P = 0.49$; Fig. 4b). Interaction of time and dispersal mode indicated a larger increase in recruitment rates of animal-dispersed compared to wind-dispersed species (Fig. 4c; repeated measures $F_{10, 840} = 7.44$, $P < 0.0001$). Individual recruitment rates also differed between animal- and wind-dispersed trees and shrubs over time (Fig. 4d; $F_{10, 840} = 1.84$, $P = 0.05$).

Interactions between treatments, life history, dispersal mode, and time showed wide differences in individual recruitment rates (Fig. 5; repeated-measures $F_{20, 840} = 2.06$, $P = 0.004$). Pioneer recruits did not differ among planting treatments (Figs. 5a and b). Later-successional animal-dispersed recruits increased in planted plots, but not in controls (Fig. 5c; $F_{20, 210} = 3.09$, $P = 0.00002$). Later-successional wind-dispersed recruits did not

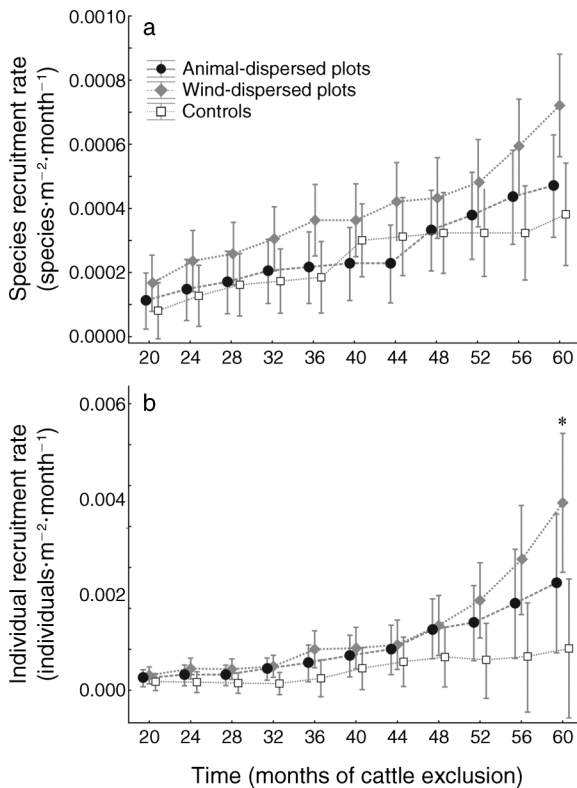


FIG. 3. Species and individual recruitment rates by planting treatment. Means are represented by circles (animal-dispersed plantings), squares (wind-dispersed plantings), and diamonds (controls). Error bars indicate 95% confidence intervals. Asterisk indicates that wind-dispersed plots show higher individual recruitment rate than controls at 60 months (Tukey test, $P \leq 0.05$).

change with planting treatments over time (Fig. 5d). High recruitment rates of later-successional individuals of species dispersed by animals (Fig. 5c) in plots of wind-dispersed trees was influenced by a precocious plot of greater soil depth (mean 42.5 cm) than other planted plots (21.5 ± 2.5 cm; \log_{10} -transformed to meet conditions of normality, $t_{14} = -7.3$, $P = 0.00001$) that formed a closed canopy at 40 months. With this outlier excluded, recruitment in stands of wind- and animal-dispersed trees were indistinguishable. Pooled planting treatments also differed from controls ($F_{10,210} = 3.68$, $P = 0.00015$).

DISCUSSION

Restoration of tropical biodiversity in abandoned pastures requires recruitment of trees from surrounding forests and forest fragments. This is true whether abandoned land is released to natural secondary succession, whether monocultures of planted trees provide conditions necessary for establishment of shade-tolerant seedlings, or whether mixed-species stands of planted trees do the same with added heterogeneity of community structure (e.g., see Aide et

al. 1995, Chazdon 2003, Butler et al. 2008). In diverse tropical landscapes, the potential advantages of planted mixed-species stands are heterogeneity of conditions for seedling establishment in addition to heterogeneity of cover and resources for potential dispersal agents. Here we test for differences in recruitment of forest tree species by successional status and dispersal mode in fenced mixed-species plantings of animal- or wind-dispersed trees and unplanted exclosures that simulate natural succession.

Characterizing the recruited community

Most tropical rain forest species do not arrive or survive in recently abandoned pastures. A common pattern is that pioneer trees with minute seeds carried by turbulent winds colonize open areas after abandonment, establishing low-diversity communities that potentially last years to decades (Janzen 1988, Zimmerman et al. 2000, Ingle 2003, Martínez-Garza and Howe 2003; see Bohrer et al. 2008). Consistent with this generalization, initial seed fall and numerical recruitment at Los Tuxtlas are heavily skewed toward wind-dispersed pioneers that establish haphazardly over the landscape or arrive but do not establish at all (Martínez-Garza et al. 2009, Howe et al. 2010). We expect that future wind-dispersed recruits will be pioneers or seedlings of planted later-successional trees, while animal-dispersed recruits will represent both planted species and increasing richness of immigrant species from nearby forest.

Challenges to restoration of biodiversity in abandoned pastures at Los Tuxtlas include seed and recruitment limitation of animal-dispersed trees from nearby forest remnants. Approximately 76% of rain-forest tree species at Los Tuxtlas are dispersed by animals (Ibarra-Manríquez and Oyama 1992). Over time one expects this majority of animal-dispersed taxa to increase because there are many more of them than wind-dispersed species. Biotically dispersed seeds carried by wide-ranging bats or birds are more mobile than any but the smallest abiotically dispersed seeds of primary-forest trees. Relevant issues for a given site are availability of seed sources of primary and old secondary forest, and how quickly rates of seed fall and particularly seedling recruitment change after pastures are abandoned.

Xeric pasture conditions and dispersal limitation pose serious impediments to restoration of tropical diversity on fallow land. High temperatures, direct solar radiation, low humidity, and little leaf litter preclude germination and establishment of many later-successional trees (Parrotta et al. 1997). Some of these do well in xeric pasture conditions if they are planted as seedlings (Martínez-Garza et al. 2005), but many do not establish from seed unless they arrive in scarce sites with enough shade and moisture to allow germination and establishment without competition from dense grasses (Otero-Arnáiz et al. 1999). Sixty months after cattle exclusion, ~15% of 300 local woody species are

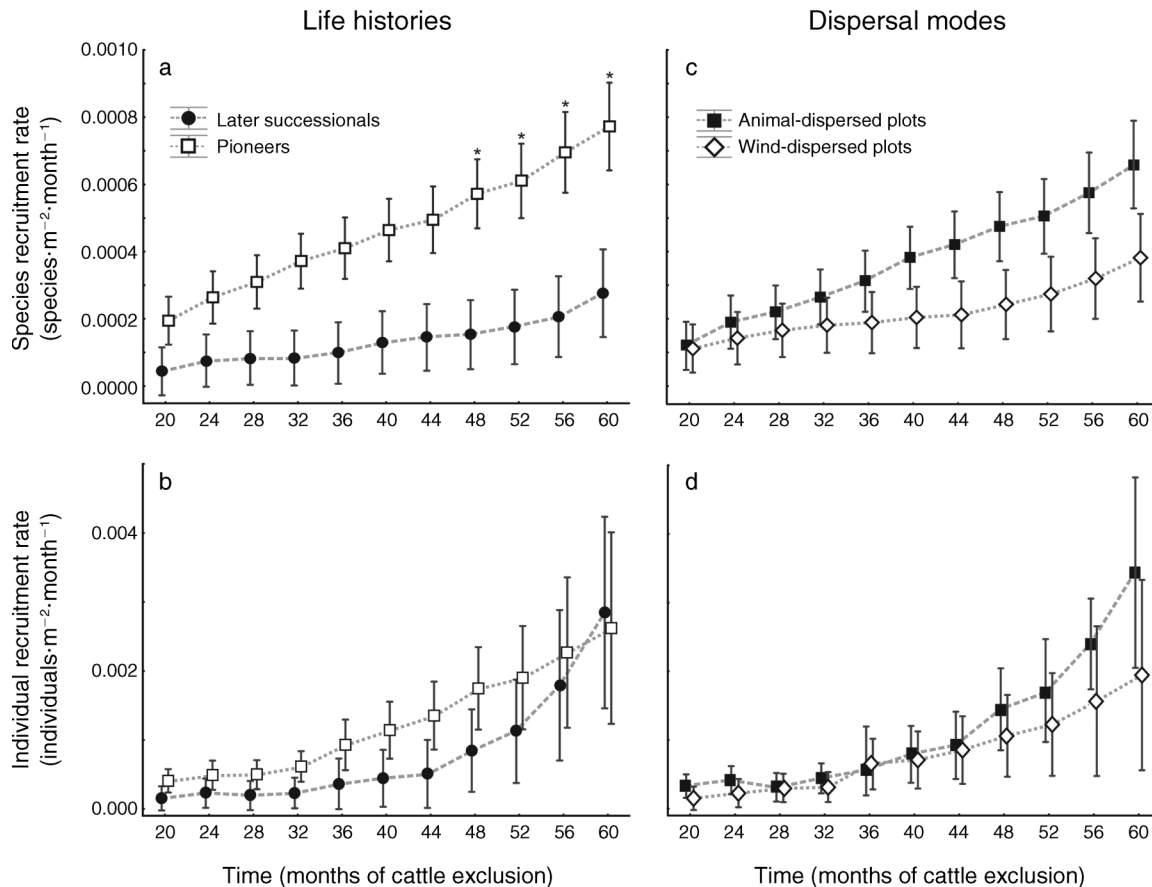


FIG. 4. Species recruitment and individual recruitment rates for tree seedlings of (a, b) pioneer and later-successional species and (c, d) animal- or wind-dispersed species. Error bars indicate 95% confidence intervals.

established in at least one of the three treatments. Low input of seeds and poor establishment of later-successional species explain this lag. Of most interest in our study, accelerating accumulation of animal-dispersed species of secondary and primary forest is evident in planted plots 48 months after cattle exclusion, but not in control plots. This likely reflects improving conditions for shade-tolerant seedlings arriving from forest 90–480 m away, and quite likely increasing attractiveness of planted plots to fruit-eating birds and mammals.

Recruitment in pastures and managed plantations

The effectiveness of seed dispersal from the plant perspective depends on where seeds land (Schupp et al. 2010). Mature tree plantations in agricultural landscapes accelerate seedling recruitment and ecological succession (Kuusipalo et al. 1995, Lugo 1997, Parrotta et al. 1997, Powers et al. 1997, Keenan et al. 1999, Chazdon 2008). In general, recruitment of woody plants into recently abandoned pastures is substantially lower than into monospecific or mixed stands of planted trees that offer shade to seedlings and cover to dispersal agents. In 15–16-year-old successional plots established on abandoned Costa Rican pastures, for instance, natural recruitment

of woody species is about half that into monospecific stands of three species, or into mixed stands of the same three species (Butler et al. 2008). Even with a clear general result, individual recruitment under some monocultures overlaps with unplanted controls, indicating the need to further clarify interactions between planted tree composition, dispersal, and recruitment.

Landscape features that attract animal dispersers into pastures play a critical role in regeneration of tropical forest (Nepstad et al. 1996, Wunderle 1997, Martínez-Garza and Howe 2003). For example, seed densities of heterospecifics in exclosures under isolated remnant trees in pastures can be as high as in the understory of continuous forest (Laborde et al. 2008). Moreover, species matter. Seedling recruitment in enclosures around isolated pasture trees is higher under sparse canopies, whether fruits are fleshy or dry (Slocum 2001). Once cattle are excluded from pastures, remnant trees become regeneration nuclei from which vegetation spreads (Holl et al. 2010). For pioneer trees, the reproductive niche of large adults is often in vegetation too dense to allow establishment of their own offspring, indicating an ontological niche shift between seedling and adult requirements (see Miriti 2006). For instance,

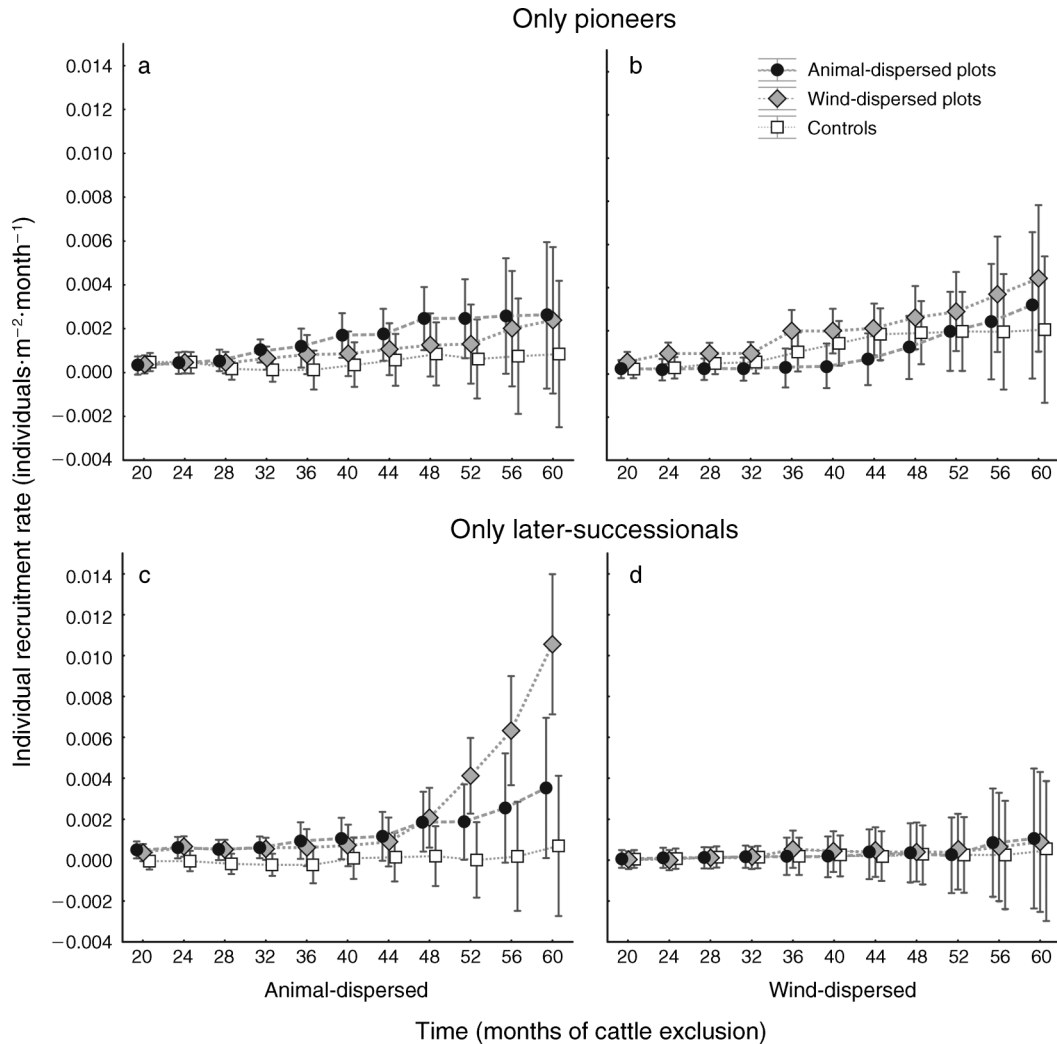


FIG. 5. Individual recruitment rates of pioneer and later-successional trees and shrubs in three planting treatments. Means are represented by circles (animal-dispersed plantings), squares (wind-dispersed plantings), and diamonds (control plots). Error bars indicate 95% confidence intervals.

large *Miconia prasina* adults in Puerto Rico recruit far more seeds in open habitats than under their own canopies (Pascarella et al. 2007). Fenced plantings that attract fruit-eating animals potentially act as buffers around or stepping stones between forest remnants for recruitment of shade-tolerant seedlings, ultimately facilitating pollen and seed exchange among forest fragments and isolated tree stands.

In the present experiment, plots remained grass covered for nearly a year following re-planting after a severe dry-season drought in 2007 killed most seedlings planted in 2006 (Martínez-Garza et al. 2011). Accordingly, cattle exclusion was the single most important factor contributing to increase of recruitment rates during the first 20 months, with substantial changes in soil and litter characteristics under a mantle of grass (Tobón et al. 2011, Roa-Fuentes et al. 2013). After 20 months, planted

stands and recruits from natural dispersal grew without interruption.

After 20 months, species recruitment rates increased steadily, with individual and species recruitment rates increasing much faster in planted stands than in controls. Most important was colonization of planted stands by later-successional trees dispersed by animals. Perches alone, without leaves or food resources, elevate seed fall of some bird-dispersed shrub and tree species, but do not necessarily elevate seedling recruitment (Holl 1998). By contrast, in our experiment individual recruitment of later-successional species accelerates steadily after 48 months following cattle exclusion in planted plots, but not in controls. A few planted animal-dispersed *Cecropia obtusifolia* and *Ficus yoponensis* and wind-dispersed *Heliocarpus appendiculatus*, *Platymiscum pinnatum*, and *Vochysia guatemalensis* reached reproductive maturity between 48 and 60 months after cattle

exclusion. Nonetheless, most individual seedling recruits (96%) were not of experimental species. Of those that were, most individuals of *C. obtusifolia* established before planted trees bore fruit. After 20 months, plantings provided resting sites, cover, and foraging sites for birds that eat both insects and fruits, and eventually provided both fruit resources for bats and birds that import seeds and environmental conditions that allowed shade-tolerant colonists from nearby forests to establish.

Plant dynamics in an agricultural mosaic

Seeds must be present for recruitment to occur, but patterns of seedling recruitment often do not closely reflect patterns of seed fall. At least 30 years of intense grazing pressure have left Los Tuxtlas pastures with little litter over thin, eroded soils (Tobón et al. 2011). In tropical soils, few woody species other than pioneers are capable of long-term seed dormancy (Dalling and Denslow 1997, Norden et al. 2009). Emerging seedlings from seed banks at our Los Tuxtlas site are primarily those of animal-dispersed trees left as legacies around stumps of figs (*Ficus* spp.) and *Bursera simaruba* that were cut during site preparation (Howe et al. 2010). Virtually all recruits (96%) of trees during the first 60 months after cattle exclusion resulted from seed dispersal at least 90–480 m from seed sources in forests or from isolated shade trees in pastures.

A simple distinction between animal- and wind-dispersed species gives insufficient weight to complexities in both dispersal modes. Wind-dispersed species, ~24% of tree species in the region, have a variety of dispersal strategies (see Wright et al. 2008). Initial colonization in the Los Tuxtlas plots has been by long-distance dispersal of species with small (<0.05 g), widely disseminated seeds of pioneers (e.g., *Cordia alliodora*, *Eupatorium galeotti*, *Heliocarpus appendiculatus*, *H. donnell-smithii*). Occasionally colonization of open ground is dominated by later-successional wind-dispersed trees with small seeds (e.g., *Tabebuia heterophylla* with 10-mg seeds in highland Puerto Rico; Zimmerman et al. 2000), but that is not the pattern at Los Tuxtlas. Aside from *Albizia purpusii*, a legacy species cut during site preparation (Howe et al. 2010), later-successional trees dispersed by wind are a negligible presence. We expect this dearth of recruitment of later-successional trees dispersed by wind to continue, other than by the eight species that we experimentally establish.

Animal behavior mediates dissemination of animal-dispersed plants. Forest birds and mammals differ in proclivity to cross open ground. Some move easily along edges, but hesitate to cross alien matrices (e.g., Levey et al. 2005); in the Los Tuxtlas landscape about 40% of 257 species of birds and mammals leave forest rarely, if at all (Estrada et al. 1993). Of the remaining 60%, many fruit-eating birds and bats live in the fragmented landscape and both distribute seeds of pioneers within the agricultural mosaic and bring seeds from forest trees into pastures

(Guevara and Laborde 1993, Galindo-Gonzalez et al. 2000). Common visitors to our plots, including large bats (*Artibeus jamaicensis*) and birds (*Ramphastos sulfuratus*), travel hundreds of meters to preferred fruiting trees (Handley et al. 1991, Graham 2001). Such long-distance commuters are most likely to bring seeds of forest trees. In 60 months of cattle exclusion, recruitment of later-successional trees shows no sign of an asymptote; quite the contrary, species recruitment is increasing and individual recruitment is accelerating.

Recruitment patterns underscore differences among ecosystems. In early secondary growth in temperate South Carolina, richness of wind-dispersed plants increases over seven years, while animal-dispersed species asymptote in five years (Damschen et al. 2008). In our study of tropical trees, dispersal limitation of later-successional trees dispersed by wind is the rule, excepting trees that we plant (Martínez-Garza and González-Montagut 1999, Martínez-Garza et al. 2009). At Los Tuxtlas, with ~100 species of fruit-eating birds and mammals and 230 species of animal-dispersed trees of old secondary and primary forest, recruitment of new species into experimental plots will continue to increase until priority effects of shade-tolerant saplings and adults suppresses newcomers (Hubbell et al. 1999). The present rate of recruitment of later-successional animal-dispersed tree seedlings remains less than one per square meter per month, with no sign of leveling off.

Future composition

Stands of trees in agricultural mosaics have the potential to increase or maintain diversity of animal-dispersed plants and fruit-eating animals that would otherwise be lost. Such habitat patches additionally may provide pollen and seed exchange among forest remnants (see Turner and Corlett 1996, Hughes et al. 2002, Kramer et al. 2008). Seeds of forest trees species will arrive, carried by birds and bats that commute from forest to feeding sites. The flora and fauna of small habitat patches will be subsets of those in continuous forest (Cordeiro et al. 2009), but at Los Tuxtlas they will be large subsets (Estrada et al. 1993, Arroyo-Rodríguez et al. 2008). Effective dispersal agents of seeds of forest trees into synthetic plant communities will be commuters from forest that fly substantial distances to and from habitat patches in which they forage, and they already appear to be bringing seeds of species that do not arrive in grassy control plots.

A caveat is that the future patterns of seed or seedling mortality within synthetic habitat patches are not yet knowable. There is no indication of density-dependent mortality among conspecific immigrant seedlings, nor is there yet evidence of density-dependent mortality across species from generalized seed or seedling predators (Howe and Smallwood 1982, Kwit et al. 2004). To date, seedling densities remain low, and what mortality occurs is likely density independent. As planted trees begin to produce large fruit crops, negative density-dependent

mortality of seeds and seedlings is certain to increase (Harms et al. 2000, Alvarez-Loayza and Terborgh 2011). The much larger pool of forest tree species likely to colonize our plots relative to planted species is likely to increase recruitment success well before density dependence occurs. Under this scenario we expect species accumulation to increase in stands of animal-dispersed trees that serve as magnets for bird and bat dispersal agents more than in stands of wind-dispersed trees that offer little food.

CONCLUSION

Sparse plantings of rapidly growing trees will have different values in different circumstances. Plantings of pioneer trees on abandoned land far from seed sources may stabilize soil, but will probably be insufficient to attract any but the most mobile fruit-eating birds and bats. Enrichment with trees bearing fruits valued by long-distance commuters, such as figs (*Ficus insipida* or *F. yoponensis*) known to large bats (*Artibeus jamaicensis*) hundreds to thousands of meters from forest, could accelerate an otherwise very slow process in planted forest stands far from seed sources.

Conversely, it is useful to ask where assisted succession is a good idea (Holl and Aide 2011). Abandoned land on deep soils near forest seed sources may well recover quickly without assistance if dispersal agents are common in the landscape. If land is abandoned or may be acquired on such sites, unassisted succession may be cost-effective. A different solution applies to land perceived as too valuable to abandon, which is the case at Los Tuxtlas. In permanent agricultural mosaics, stepping-stone forest patches could serve an important function in maintaining "countryside diversity" of both plants and animals (Turner and Corlett 1996, Daily et al. 2001, Hughes et al. 2002), while preserving a degree of connectivity during a period of historically rapid climate change (Corlett 2011). On our site, unassisted succession is slow; planted trees that grow rapidly are likely to increase recruitment of animal-dispersed trees of old secondary and primary forest, ultimately providing stands of young adult trees of many species that provide food for fruit-eating animals, mates through long-distance pollination for widely dispersed "populations" of trees (Kramer et al. 2008), and seed exchange among small forest fragments and larger remnants. Stepping-stone patches, more widely spaced than our experimental design permits, may serve a critical purpose in maintaining connectivity among forest fragments and maintaining biodiversity in highly altered landscapes.

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SUPPLEMENTAL MATERIAL

Appendix A

Selection of planted species (*Ecological Archives* A023-059-A1).

Appendix B

Recruited species in agricultural pasture of Los Tuxtlas, Mexico (*Ecological Archives* A023-059-A2).