FACTORS AFFECTING COMMUNITY COMPOSITION OF FOREST REGENERATION IN DEFORESTED, ABANDONED LAND IN PANAMA

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Abstract. We tested alternative hypotheses concerning factors affecting early forest succession and community composition in deforested and abandoned areas invaded by an exotic grass, *Saccharum spontaneum*, in Panama. We hypothesized three barriers to natural regeneration: (1) *Saccharum* competition, (2) seed dispersal limitations, and (3) fire. We measured natural tree and shrub regeneration in a factorial experiment combining distances from adjacent forest, mowing treatments of the *Saccharum*, and a prescribed burn. To determine the applicability of the general model of neotropical succession and the nucleation model of succession to species composition of forest regeneration in these anthropogenic grasslands in Panama the effect of time since fire and distance to remnant vegetation (isolated trees, shrubs, and large monocots) was measured.

Fire significantly affected species composition and decreased species richness because most species had either their resprouting ability or seed germination inhibited by fire; the few species that had regeneration enhanced by fire dominated early successional communities. Sites differed in time since fire, ranging from 1 to 4 yr; the interaction of site and distance from the forest significantly affected community composition and the prevalence of species with different dispersal mechanisms and shade tolerance. At recently burned sites, light-dependent wind-dispersed species predominated; most were found near the forest edge. As time since fire increased, significantly more shade-tolerant, larger-animal-dispersed species were recorded, and the proximity to and species identity of remnant vegetation became more important in affecting species composition of the natural regeneration; no significant effect of distance from the forest was found at sites that were unburned for three or more years. Our results support both successional models; the temporal sequence of species composition corresponded to later stages of the general model, while the spatial distribution of species followed the nucleation model. Our results highlight the importance of effective seed dispersal in structuring successional species composition and distribution and in regaining lost diversity resulting from frequent fires in the *Saccharum*.

Key words: abandoned farmland; anthropogenic grassland; natural regeneration; Panama; remnant forest; Saccharum spontaneum; *secondary succession; seed dispersal; tropical forest.*

INTRODUCTION

Extensive deforestation in the tropics has produced vast areas of land in various stages of grassland and secondary succession, accounting for over 40% of the total tropical forested area (Brown and Lugo 1990). Species richness may recover rapidly during secondary forest succession; however, the species composition of secondary forest remains very different from that of mature forest for many decades (Brown and Lugo 1990, Finegan 1996). The processes determining which species invade and participate in succession on deforested sites in the tropics remain poorly understood (Wijdeven and Kuzee 2000). Most knowledge on secondary forest succession is based on research in temperate areas;

these models are often directly applied to tropical systems. However, successional models developed in temperate areas do not include stochastic factors such as seed availability and dispersal (Finegan 1984, McCook 1994), and therefore they may have limited application for understanding succession in tropical areas where most tree species are animal-dispersed (Howe and Smallwood 1982). Research suggests that these models may even be misleading when applied to tropical ecosystems because some of the major seed dispersers in the tropics (frugivorous primates, large frugivorous birds and bats) are absent from temperate areas (Chapman and Chapman 1999).

A widely applied model of forest succession in neotropical systems is an interpretation of the initial floristic composition model of Egler (1954) (complete initial floristics sensu Wilson et al. [1992]), in which the species participating in a succession become established at or soon after initiation (Finegan 1984,

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1996). Successional change is the sequential physiognomic dominance of the site by these species because of differences in their growth rates, shade tolerance, longevity, and size at maturity (Finegan 1984, 1996). According to this model applied to tropical forest ecosystems, succession following disturbance has four stages (defined by the form and duration of their dominant species): (1) herbs, shrubs, and climbers (initial colonization), (2) short-lived pioneers (10–30 yr), (3) long-lived pioneers (75–150 yr), and (4) shade-tolerant species (mature forest) (Finegan 1996, Guariguata and Ostertag 2001). The light-demanding species of the first three stages arrive early after disturbance, while shade-tolerant species colonize continuously and eventually replace the long-lived pioneers. Life history variation and competition among species are thought to drive successional change; however, Finegan (1996) states that this cannot completely explain succession because the presence of a tree species in the later stages of succession depends on factors operating early in succession, including initial site conditions and seed dispersal. Finegan (1996) states that for progress to be made towards understanding floristics during the first century of rain forest succession, experimental studies of the regeneration of long-lived species on recently abandoned land are needed; the present study addresses this need.

Species composition during secondary succession of deforested areas that have been used for agriculture and subsequently abandoned often does not follow such predictable successional trajectories because prior land use generally causes land degradation (Guariguata and Ostertag 2001). Succession is often delayed in proportion to the intensity of prior land use (Uhl et al. 1988, Aide et al. 1995). The suite of species characteristic of early succession on these abandoned, degraded tropical lands may differ from those predicted by the general successional model because of interactions between site-specific factors and land use; these colonizers may facilitate, inhibit (sensu Connell and Slatyer [1977]), or even divert succession depending upon land use before abandonment (Mesquita et al. 2001). These abandoned agricultural lands are often invaded by exotic grasses, which can constrain or arrest succession of tree species because of recurrent fires (D'Antonio and Vitousek 1992). Grass competition can prevent many tree species from regenerating, especially small-seeded species, thus affecting plant community composition (Nepstad et al. 1990, 1996, Hooper et al. 2002). Also, recovery of mature-forest species composition on heavily used sites can be very slow (Guariguata and Ostertag 2001) because intensive land use (often coupled with fire) eliminates tree regeneration from the seed bank and root sprouts (Uhl et al. 1988, Nepstad et al. 1990), leaving seed dispersal as the critical mechanism for forest regeneration. However, seed dispersal may be limited because most frugivores will not travel into large, abandoned areas (Cardosa da Silva

et al. 1996); those that do rarely venture far from the forest edge (Aide and Cavelier 1994). Insufficient seed dispersal is therefore a major factor impeding tropical secondary forest regeneration at many neotropical sites (Uhl et al. 1988, Aide and Cavelier 1994, Holl 1999, Holl et al. 2000, Wijdeven and Kuzee 2000, Zimmerman et al. 2000). Consequently, early secondary succession follows the nucleation model of succession at many tropical sites (sensu Yarranton and Morrison [1974]) because remnant trees (Guevara et al. 1986, Guevara and Laborde 1993), shrubs (Vieira et al. 1994, Holl 2002, but see Zahawi and Augspurger [1999]), and large-leaved monocots (Duncan and Chapman 1999) can attract seed dispersers and facilitate native rain forest regeneration under their canopies.

In this study, we investigate hypothesized factors affecting the early stages of secondary forest succession on abandoned agricultural lands in central Panama; these areas originally supported mature tropical moist forest. In Panama, many abandoned agricultural sites are invaded by a tall (2.5 m), exotic grass species, *Saccharum spontaneum* L. subsp. *spontaneum* (wild sugarcane, paja blanca), which grows in dense, impenetrable stands. Throughout the text, we refer to these areas in Panama that have been deforested, used for agriculture, abandoned, and then invaded by *Saccharum* as grassland. It is thought that *Saccharum* was introduced into Panama between 1950 and 1960; it was reported in the canal zone in 1978 (Croat 1978). *Saccharum spontaneum* is highly invasive, adapted to drought, burns frequently, and has deep rhizomes that make it difficult to eradicate through such treatments as weeding, deep plowing, and fire (Panje 1970). It originated in the sub-Himalayan valleys as an innocuous species but migrated to the central Indian plateau where it evolved a highly rhizomatous ecotype that is listed as one of the most serious weeds in Indonesia, India, and Thailand and a principal weed in the Philippines and Puerto Rico (Holm et al. 1979). It has been postulated that *Saccharum* stands prevent succession of forest species in Panama (Aide and Cavelier 1994); however experimental evidence for this effect is lacking (but see Hooper et al. [2002]).

We hypothesized that low seed dispersal, competition with *Saccharum spontaneum*, and fire affect species composition of early forest regeneration; we used a multi-factorial experimental design to test the importance of these factors. First, the effect of distance from the forest edge was assessed to evaluate the role of potential limitations to seed dispersal. Second, competition with *Saccharum spontaneum* was studied by comparing mown and unmown treatments. Third, the effect of fire was investigated by performing a prescribed burn. Tree and shrub sprouts, seedlings, and saplings were monitored over a 1-yr period beginning in August 1996 to assess the effects of these factors on natural regeneration. To determine the significance of these experimental factors and their interactions in

affecting species composition we used a recently developed multivariate statistical method, distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999); in a companion paper, we investigated the effect of these factors on the density and species richness of tree species recruitment (E. Hooper, P. Legendre, and R. Condit, *unpublished manuscript*). Distance-based redundancy analysis is advantageous for a variety of reasons, especially for tropical data characterized by a high number of rare species (Appendix A). To determine the effect of fire on successional vegetation development, we used a chronosequence approach by studying floristic composition on plots at sites with known time since fire (Appendix A). We relate our results to previous tropical successional hypotheses, namely, the initial floristic composition model (proposed by Egler [1954] and applied to tropical succession by Finegan [1996]) and the nucleation model (Yarranton and Morrison 1974). To evaluate the importance of succession following the nucleation model, we determined the effect of remnant trees, shrubs, and large-leaved monocots found in the *Saccharum* grasslands on natural tree and shrub regeneration by documenting their locations and measuring their proximity to each naturally regenerating seedling.

MATERIALS AND METHODS

Study site

Las Pavas (9°06′ N, 79°53′ W) is located near the Panama Canal, 4 km southwest of the Barro Colorado Nature Monument (BCNM), where the Smithsonian Tropical Research Institute reserve is located. The Nature Monument supports a tropical moist forest type (Croat 1978) as did the study area prior to deforestation, which began in 1976 (Penna Franco 1990). By 1984, most of the land had been burned, used for subsistence agriculture, and then abandoned before 1990. Once abandoned, the land was invaded by the introduced, exotic grass *Saccharum spontaneum*. It grows in dense, monotypic stands interspersed with patches of forest (tree islands) that were spared during deforestation, for example in corridors along streams. Within these *Saccharum* grasslands, remnant vegetation such as isolated trees, shrubs, and large-leaved monocots (*Musa* and *Heliconia* spp., to which we refer as large monocots) are also occasionally present. The study area is moderately hilly.

Rainfall at the BCNM averages 2600 mm, with a pronounced dry season from mid-December until mid-April (Windsor 1990). Rainfall was above the mean for the first wet season of the study (1996), but was well below the mean during the 1997 dry season (Smithsonian Environmental Sciences Project, *unpublished data*).

Experimental design

Five sites, located 0.6–3.4 km apart, were chosen for experimentation. Each site was located in an area dominated by *Saccharum spontaneum* and adjacent to a different tree island, which we refer to as a forest edge. A transect perpendicular to each forest edge was extended into the *Saccharum*-dominated grassland. Plots were located with their midpoints at 10, 35, and 85 m along the transect. Each plot consisted of three 12 × 12 m subplots for the three treatments: mowing the *Saccharum* once, mowing three times, and control (no mowing; Appendix B). The location of each treatment within each distance from the forest edge was selected by random draw. Treatments were implemented by hand-cutting the *Saccharum* with machetes in July 1996 (once mown) and additionally at intervals 4 mo apart in November 1996 and March 1997 (thrice mown). All subplots were subdivided into 25 sub-sub-plots (each 2 × 2 m) with a 0.5-m trail between them to facilitate measurement of tree seedlings and cutting the *Saccharum* without damaging the tree and shrub regeneration. All individual trees and shrubs found within these plots were monitored for a year at four regularly spaced census intervals: August 1996 (mid-wet season), December 1996 (end of wet season), April 1997 (late dry season), and mid-July 1997 (early wet season). Each tree and shrub seedling and sapling encountered was identified to species, marked with an aluminum tag, and mapped. Origin as root sprout was recorded whenever possible (we had difficulty determining the origin of less than 2% of the seedlings).

To study the effect of fire and its impact upon native tree species regeneration, the same experimental design as detailed above was repeated at each site 20–50 m from the preexisting experimental plots. A 15-m firebreak was cut and maintained between the unburned plots and those plots subject to a prescribed burn during April 1997 (peak fire season). At each site, the entire experimental design, including the plots to be burned and those to remain free of fire, was surrounded by a 20–25 m firebreak (Appendix B). Despite these precautions, uncontrolled anthropogenic fires crossed the firebreaks at two sites after the third census data had been collected, burning both sides. This affected subsequent statistical analyses, which will be detailed in *Statistical analyses*. All prescribed burns were successful, and all individual trees and shrubs found within these plots were monitored for a year at four census intervals (two prefire and two postfire) following the same methodology and timing as for the unburned plots.

To determine the effect of remnant vegetation on seedling abundance, we located, identified, and mapped all vegetation taller than 2.5 m in the *Saccharum* at these sites. We measured the distance of each naturally regenerating tree and shrub seedling to each isolated tree, sapling, shrub, or large monocot. To determine the importance of time since fire, at each site the number of months between the last wildfire and July 1996 was determined by interviewing 12 persons familiar with the study area. Personal observations of charred

Saccharum and charred trees were used to verify the survey information; we believe that these observations could accurately identify areas that had been burned up to two years prior to our experiments. We also measured *Saccharum* biomass and litter: the standing biomass of a 1×1 m subsample of live *Saccharum spontaneum* and the biomass of the litter in the same subsample were separately collected for each subplot, at each site, in July 1997. Samples were dried and the dry mass recorded to the nearest gram.

Statistical analyses

Effect of distance from the forest, Saccharum *competition, time, site, and fire on community composition.*—Distance-based redundancy analysis (db-RDA; Legendre and Anderson 1999) was used to test the significance of the experimental factors and their interaction terms in three-way ANOVA models, using species assemblage as the response variable; the factors site, time, and fire were separately crossed with *Saccharum* competition and distance from the forest. Details and justification of the methods used are presented in Appendix A.

Effect of time since fire.—To test the significance of time since fire on species composition and relate it to our experimental factors, forward selection of the variables (time since fire, distance from the forest, and *Saccharum* biomass) was performed using redundancy analysis (RDA) of appropriately transformed data; details are found in Appendix A.

Effect of proximity to remnant vegetation.—Remnant vegetation was grouped into three classes: (1) large monocots, (2) isolated trees (height >5 m), (3) shrubs and saplings (2.5–5 m in height). We determined the relative effects of distance from the forest, the three remnant vegetation classes (biotic factors), *Saccharum* biomass, and time since fire (abiotic factors) on the overall density and species richness of natural regeneration, as well as on the distribution of each species found in more than 5% of the subplots. For each species, we first tested which shape of the curve relating the number of naturally regenerating individuals to distance from each potential seed source or dispersal attractant explained the most variation. We utilized the two most common functions: the inverse power function and the negative exponential function (Okubo and Levin 1989) as well as a truncated normal distribution (Peart 1985). In almost all cases, we found that the negative exponential function represented by the equation $y = ae^{-bx}$ (where y is seedling density, x is distance from the source, a and b are constants, and e is the Napierian number) yielded the best fit (assessed by comparing R^2 coefficients); only those regression results are reported. To determine the relative importance of distance to the forest and distance to each vegetation class (biotic), as well as the abiotic factors on the density of each species, we used a backward selection procedure in nonlinear regression analysis (Proc NLIN,

SAS 1988), retaining only those variables significantly ($P < 0.05$) affecting each species' density. In each model we included the linear and negative exponential terms for each biotic factor and the linear term for each abiotic factor. When both the abiotic and biotic factors were significant, we used a partialling analysis (Borcard et al. 1992) to assess their relative importance to the total variance explained.

Relationship of species characteristics to habitat variables.—Fourth-corner analyses were performed to analyze which characteristics of the species were significantly related to time since fire and distance from the forest at the sites; the procedure is outlined in Legendre et al. (1997). We assessed, by permutation testing, whether the correlations between variables were significantly different from the values they would have had in a randomly organized environment. The permutation model can vary depending on the ecological model; permutation model 1 (environmental control over individual species, effected by permuting each row vector [Legendre et al. 1997]) was chosen as the most appropriate for our analyses. The tested species characteristics were: (1) seed size (in millimeters); (2) shade tolerance as calculated in Condit et al. (1996); (3) resprout index, calculated as the number of individuals originating from root sprouts/total number of individuals; (4) adult size class, with four categories as defined in Condit et al. (1995) (tree, mid-sized tree, understory treelet, shrub); (5) dispersal vector or mechanism with seven categories; we grouped the naturally regenerating species into seven major categories according to relevant dispersal characteristics including their primary and (if applicable) secondary dispersal mechanism or vector (R. Foster and R. Perez, *personal communication*): (1) wind-dispersed, not reproducing in *Saccharum* grasslands; (2) wind-dispersed, reproducing in grasslands (there is a single species in this group, *Cochlospermum vitifolium*); (3) ballistic dispersal (explosion); (4) small-bird-dispersed (seed size <10 mm); this group of plants may also be dispersed by bats and other mammals; (5) bat-dispersed (there is a single species in this group, *Piper marginatum*; it is known to be exclusively bat-dispersed); (6) arboreal animal-dispersed (seed size >10 mm), including dispersal by large birds and arboreal frugivores; (7) secondarily agouti-dispersed (there is a single species in this group, *Gustavia superba*; it is known to be scatterhoarded by agoutis, *Dasyprocta punctata*). In a first analysis, we analyzed the relationship between time since fire and distance from the forest with three species characteristics (seed size, shade tolerance, and resprout index). In a second analysis, we tested the relationship between dispersal mechanism or vector and time since fire, and in a third we analyzed the relationship between adult size class and time since fire.

RESULTS

Background information.—We found 4984 individuals of 80 woody species naturally regenerating in these

Saccharum grasslands (Appendix C). There were significantly more species at 10 m from the forest than at 35 m from the forest (85 m was intermediate) after the first census. For example, in December 1996 we recorded 7.06 ± 0.75 species/10 m^2 at 10 m from the forest, 3.27 ± 0.7 species/10 m^2 at 35 m, and 4.86 ± 0.90 species/10 m^2 at 85 m. Fire significantly decreased the number of species from 6.22 ± 0.93 species/10 m^2 prefire to 2.83 ± 0.58 species/10 m^2 postfire (E. Hooper, P. Legendre, and R. Condit, *unpublished manuscript*). The most common species, in descending order of importance (total number of individuals) were *Gustavia superba* (1060), *Piper marginatum* (522), *Cochlospermum vitifolium* (400), *Spondias mombin* (290), *Cordia alliodora* (241), *Cecropia insignis* (237), *Byrsonima crassifolia* (196), *Inga vera* (182), *Banara guianensis* (181), *Trichospermum galeotti* (174), *Trema micrantha* (161), *Swartzia simplex* (var. *ochnacea*) (158), and *Hybanthus prunifolius* (141) (Appendix C).

Seedling density was significantly lower in the first census (August 1996: 14.74 ± 3.07 individuals/10 m^2) than in all subsequent censuses in which density doubled to tripled depending on the season (dry season, April 1997, 28.48 ± 6.06 individuals/10 m^2; wet season, December 1996, 35.41 ± 7.86 individuals/10 m^2; August 1997, 33.74 ± 7.10 individuals/10 m^2). Recruitment was significantly reduced during the dry season falling from a mean of 19.04 ± 5.42 recruits/10 m^2 in December 1996 to 3.11 ± 0.88 recruits/10 m^2 in April 1997. Tree and shrub density was not significantly affected by distance from the forest or *Saccharum* treatment and fire did not significantly decrease the number of individuals when all seedlings regardless of origin were included in the analysis. However, when root sprouts were excluded, fire reduced mean seedling density from 28.22 ± 8.1 seedlings/10 m^2 to 11.61 ± 4.3 seedlings/10 m^2. The percentage of seedlings originating as root sprouts increased in recently burned plots (unburned, $31.30 \pm 7.30\%$; burned, $51.82 \pm 10.20\%$) (data from E. Hooper, P. Legendre, and R. Condit [*unpublished manuscript*]).

Effect of distance from the forest, Saccharum *competition, time, site and fire.*—

1. *Site, distance from the forest.*—Community composition significantly differed depending upon distance from the forest, as did recruitment; these species differences depended upon site (db-RDA; effect of site $\times$ distance interaction on community composition, $P = 0.001$, 12.2% of the variance explained; recruitment, $P = 0.001$, 12.4% of the variance explained). Three sites (A, B, C) had significant differences in community composition with respect to distance from the forest (Fig. 1). These sites supported early postfire communities; wildfires burned site A 1 yr before data collection, whereas sites B and C were burned 2 yr prior to data collection. In contrast, the sites surveyed 3 (site D) and 4 yr (site E) after fire showed no significant

effect ($P = 0.119$, $P = 0.116$) of distance from the forest on community composition.

One year postfire (site A), different light-dependent, wind-dispersed species dominated the communities, with significantly different community composition and recruitment at 10 m from the forest (*Trichospermum galeotti* and *Luehea seemannii*) and 85 m from the forest (*Cochlospermum vitifolium*) (Fig. 1a). Light-dependent, small-bird-dispersed species were important at 10 m (*Cecropia insignis*, *Miconia argentea*) and 85 m (*Trema micrantha*) from the forest. In contrast, the bat-dispersed *Piper marginatum* dominated at 35 m from the forest. Few large-animal-dispersed species were present (*Spondias mombin*, *Swarzia simplex*, and *Gustavia superba*) and these resulted mainly from resprouting. There was no remnant vegetation (large monocots, trees, or shrubs) at this site.

Two years after fire, there were fewer wind-dispersed and small-bird-dispersed species near the forest, while the wind-dispersed *Cochlospermum vitifolium* had increased in density and height at 85 m from the forest. In contrast to 1 yr after fire, remnant vegetation such as isolated trees, saplings, shrubs, and large monocots were found at some of the sites; this vegetation affected seedling community composition wherever present. For example, at site B, the 10-m and 85-m distances had significantly ($P < 0.002$) different community compositions and major differences in density of large monocots at these distances; plots at the 35-m distance significantly differed from neither (Fig. 1b). Large monocots were very abundant at 10 m from the forest, and their density declined with distance from the forest; the density of the agouti-dispersed *Gustavia superba* mirrored this decline. It dominated the plant communities at 10 and 35 m from the forest. Some wind-dispersed (*Trichospermum galeotti*, *Cordia alliodora*), explosion-dispersed (*Croton billbergianus*), and small-bird-dispersed (*Miconia argentea*, *Psychotria grandis*) species were also found at these distances. In contrast, there were very few of these species at 85 m from the forest; this community was dominated by *Cochlospermum vitifolium*. At site C, large monocots and isolated trees were located at 10 and 85 m from the forest, while none were located at 35 m from the forest. The community at 35 m was significantly different from those at 10 and 85 m from the forest, which did not significantly differ from one another (Fig. 1c). At 10 and 85 m, large-arboreal-animal-dispersed (*Byrsonima crassifolia* and *Cordia bicolor*), wind-dispersed (*Cochlospermum vitifolium*, *Tabebuia guyacan*, and *Cordia alliodora*) and agouti-dispersed (*Gustavia superba*) species were important. At 35 m from the forest, there were few species except the bat-dispersed *Piper marginatum*.

2. *Fire.*—Fire did not significantly change the overall community composition when all seedlings regardless of origin were included in the analysis, or when individuals originating as root sprouts were analyzed.
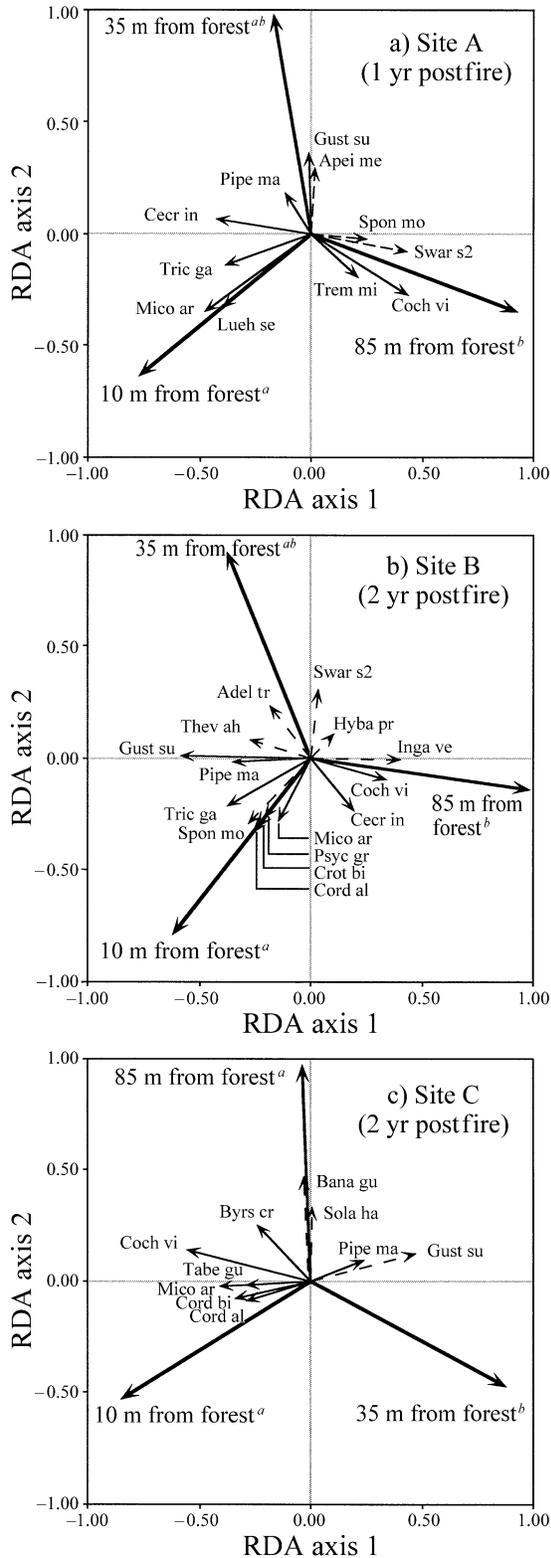
In contrast, when root sprouts were excluded from the analysis, fire significantly changed community composition (db-RDA; $P = 0.001$), explaining 21.1% of the species variance. Therefore, differences in community composition after fire resulted from the effect of fire on recruitment from seed; however the effect of resprouting predominated, maintaining the overall community composition.

Species differed in the effect that fire had on the amount of regeneration from resprouts and recruits (from seed); these differences had a significant impact upon community composition (db-RDA; $P = 0.001$). Many more species showed a decline in one or both mechanisms of regeneration compared to those that increased in response to fire, leading to a decreased number of species as a result of fire (Table 1). One species increased in resprouting and recruitment from seed following fire, 14 species decreased in both, and some had an increase in one mechanism of regeneration, while the other decreased. Ten species had increased recruitment from seed following fire, but only two (*Trema micrantha* and *Byrsonima crassifolia*) substantially contributed to increasing seedling density. In contrast, 43 species had decreased recruitment from seed as a result of fire; 18 of these did not resprout, while 11 had increased resprouting after fire. It was these latter species, especially *Gustavia superba*, *Cochlospermum vitifolium*, and *Cordia alliodora*, that maintained community composition following fire, despite the difference in how they regenerated.

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FIG 1. Redundancy analysis (RDA) ordination biplots illustrating the effect of distance from the forest on community composition for the three sites in Las Pavas, Panama, where species composition was found by db-RDA to be significantly ($P < 0.05$) affected by distance from the forest. The three sites are arranged in order of increasing time since fire. Similar superscripts for the factor levels indicate no significant difference ($P < 0.05$) in community composition, following post hoc planned comparisons. Species represented by dashed lines are those regenerating by root sprouting. (a) Significant ($P = 0.027$) effect of distance from the forest on community composition at site A, explaining 17.0% of the total variance. (b) Significant ($P = 0.040$) effect of distance from the forest on community composition at site B, explaining 15.9% of the total variance. (c) Significant ($P = 0.004$) effect of distance from the forest on community composition at site C, explaining 19.0% of the total variance. Species codes: Apei me = *Apeiba membranaceae*, Adel tr = *Adelia triloba*, Bana gu = *Banara guianensis*, Byrs cr = *Byrsonima crassifolia*, Cecr in = *Cecropia insignis*, Coch vi = *Cochlospermum vitifolium*, Cord al = *Cordia alliodora*, Cord bi = *Cordia bicolor*, Crot bi = *Croton billbergianus*, Gust su = *Gustavia superba*, Hyba pr = *Hybanthus prunifolius*, Inga ve = *Inga vera*, Lueh se = *Luehea seemannii*, Mico ar = *Miconia argentea*, Pipe ma = *Piper marginatum*, Psyc gr = *Psychotria grandis*, Sola ha = *Solanum hayesii*, Spon mo = *Spondias mombin*, Swar s2 = *Swartzia simplex* var. *ochnacea*, Tabe gu = *Tabebuia guyacan*, Thev ah = *Thevetia ahouai*, Trem mi = *Trema micrantha*, Tric ga = *Trichospermum galeotti*.

TABLE 1. The effect of fire on the number of recruits (from seeds), the number of resprouts, and the total number of individuals found naturally regenerating at burned sites at Las Pavas, Panama.

Species	No. species	Recruits		Resprouts		Total	
		Before fire	After fire	Before fire	After fire	Before fire	After fire
Resprouts and recruits increased							
Thevetia ahouai	1	8	20	1	25	9	45
Recruits increased, no resprouts							
Trema micrantha		3	150	0	0	3	150
Byrsonima crassifolia		36	62	0	0	36	62
Total	10	52	276	0	0	52	276
Resprouts increased, no recruits							
Total	3	0	0	4	9	4	9
Recruits decreased, resprouts increased							
Gustavia superba		426	117	157	300	583	417
Cochlospermum vitifolium		105	82	22	125	127	207
Cordia alliodora		24	9	56	122	80	131
Total	11	622	225	317	751	939	976
Recruits decreased, no resprouts							
Piper marginatum		300	32	0	0	300	32
Cecropia insignis		68	3	0	0	68	3
Total	18	465	56	0	0	465	56
Recruits and resprouts decreased							
Banara guianensis		8	1	90	50	98	51
Hybanthus prunifolius		53	4	41	33	94	37
Inga vera		21	0	69	45	90	45
Swartzia simplex var. *ochnacea*		23	0	40	6	63	6
Total	14	160	6	269	140	429	146
Overall total		1307	583	591	925	1898	1508

Notes: Species are grouped into categories depending upon their regeneration response to fire. Only those species that contributed significantly to the overall community abundance are listed.

3. *Time.*—Short-term variation was not an important determinant of community composition. Neither time, nor its interaction with *Saccharum* treatment or distance from the forest, significantly affected community composition.

4. Saccharum *competition.*—Mowing the *Saccharum* caused significant changes in species composition; these differences depended upon distance from the forest (db-RDA; distance × treatment interaction, $P < 0.001$). These species differences resulting from different distances from the forest were significant for all treatments: $P < 0.001$ (thrice mown), $P < 0.001$ (once mown), and $P < 0.003$ (unmown control). However, the variance explained by this interaction was low ($<5\%$) and therefore we do not want to emphasize these results. The main difference between treatments was that when the *Saccharum* was mown, more agouti-dispersed seedlings were present at the 85-m distance than when it was unmown.

Effect of time since fire.—Time since fire significantly affected community composition ($P = 0.016$), as did distance from the forest ($P = 0.038$), live *Saccharum* biomass ($P = 0.001$), and dead *Saccharum* litter ($P = 0.001$); this model explained 11.7% of the species variance.

Effect of proximity to remnant vegetation in the Saccharum.—Distance from the forest and large monocots

significantly and negatively affected the number of species encountered ($F_{4,87} = 7.24$; $R^2 = 67.9\%$) (Appendix D). Distance from the large monocots was the only factor significantly affecting overall seedling density ($F_{3,87} = 22.65$; $R^2 = 56.6\%$); seedling density declined as distance from the large monocots increased. Wind-dispersed species were affected by distance from the forest and time since fire. The two most abundant wind-dispersed species, *Trichospermum galeotti* and *Luehea seemannii*, had declining densities with distance from the forest. Time since fire significantly and negatively correlated with the density of the wind-dispersed *Trichospermum galeotti* and *Cochlospermum vitifolium*. In general, the density of the small-bird-dispersed species (*Miconia argentea*, *Psychotria horizontalis*) was negatively correlated with distance from isolated trees while the large-arboreal-animal-dispersed species had densities that were affected by distance from the forest (negatively correlated, *Thevetia ahouai*, *Inga vera*; positively correlated, *Swartzia simplex*). The density of *Byrsonima crassifolia*, a large-bird-dispersed species, declined significantly as distance from saplings and shrubs increased. The densities of the bat-dispersed *Piper marginatum*, the bat- and small-bird-dispersed *Cecropia insignis*, and the secondarily agouti-dispersed *Gustavia superba* declined exponentially as distance from large monocots increased; this effect explained a

large proportion (57.7, 33.5, and 44.9%, respectively) of the variation in their densities.

Relationship of species characteristics to habitat variables.—The wind-dispersed *Cochlospermum vitifolium* was found more often in recently burned plots (negative correlation of time since fire and presence of *Cochlospermum vitifolium*; $P = 0.008$), whereas large-animal-dispersed species and species regenerating from root sprouts were found in higher proportions as time since fire increased (positive correlation of time since fire with the presence of large-arboreal-animal-dispersed species and species with a high resprout index; $P = 0.008$) (Appendix E). More pioneer species and species regenerating from seed were found in recently burned plots; as time since fire increased, more shade-tolerant species were found, many of which regenerated by resprouting (time since fire negatively correlated with light index and positively correlated with resprout index; $P = 0.001$) (Appendix F). Small-seeded species were found close to the forest, while large-seeded species were found further from the forest (seed size positively correlated with distance from the forest; $P = 0.025$). Seedlings of medium-sized trees were found in recently burned plots; as time since fire increased, more shrubs were found (time since fire was negatively correlated with the presence of medium-sized trees and positively correlated with the presence of shrubs; $P = 0.004$ and $P = 0.015$, respectively) (Appendix G).

DISCUSSION

Our results emphasize the predominant effect of fire and limitations of effective seed dispersal (a combination of dispersal and survival) in affecting species composition and density of naturally regenerating trees and shrubs in *Saccharum*-dominated abandoned land in Panama. Fire is a major barrier to natural forest regeneration because it decreases species richness. Fire causes a decline in the number of species recruiting from both the seed bank and resprouting, leading to an impoverished community, as has been similarly documented at other tropical sites (Uhl et al. 1988, Nepstad et al. 1990). More species have decreased recruitment from seed (43) than those with enhanced recruitment after fire (11), while half of the species able to resprout have lowered or no resprouting following fire. Suboptimal resprouting after fire is reported at other neotropical sites (Uhl et al. 1990, Kauffman 1991, Sampaio et al. 1993, Miller and Kauffman 1998).

With this low seed bank recruitment and suboptimal resprouting, seed dispersal is the critical mechanism of forest regeneration; over 75% of the natural regeneration originates from recently dispersed seeds in plots that do not receive a prescribed burn. Species richness and density are highly influenced by spatial factors. Proximity to both forest and large monocots significantly and positively affects overall species richness, accounting for 68.1% of the variation. Different species are found near the forest compared to those found near the large monocots. In Costa Rica, Slocum (2001) also found that the species identity of remnant vegetation in abandoned pastures affected the species composition of regeneration below them. At our sites, more species are significantly affected by proximity to the forest, including most of the larger-arboreal-animal-dispersed, wind-dispersed, and ballistic-dispersed species; these species have either a negative linear or negative exponential decline in seedling density with distance from the forest. In contrast, the highest density of natural regeneration is found in close proximity to large monocots; three of the most common species (accounting for 42% of the total density of all naturally regenerating individuals) are found in high densities close to the large monocots including the bat-dispersed *Piper marginatum*, the agouti-dispersed *Gustavia superba*, and *Cecropia insignis*, which is reported to be both bird- and bat-dispersed (Dalling et al. 1998b, Medellin and Gaona 1999). Their seedlings had a negative exponential decline with distance from these monocots. Agoutis eat bananas (Murie 1977), and bats use them for feeding roosts (E. Hooper, *personal observation*); these facts may account for their high densities near the large monocots. Other remnant vegetation, including shrubs, saplings, and trees found in these *Saccharum* grasslands, also affects the species composition of seedlings regenerating in close proximity. Seedling densities of the large-bird-dispersed *Byrsonima crassifolia* decline linearly with increasing distance from shrubs and saplings, while seedlings of the small-bird-dispersed species *Miconia argentea* and *Psychotria horizontalis* have exponentially declining densities with distance from remnant trees.

These results suggest that proximity to forest and different remnant vegetation classes in the grasslands differentially affects seed dispersal vectors, resulting in spatially distinct variations in community composition in relation to this vegetation. Seed dispersal therefore appears to be critical in determining the diversity, density, and location of natural regeneration. However, we could not distinguish whether higher densities of seedlings under forest and remnant vegetation are due to elevated seed rain, increased survival, or a combination of these factors because we studied the effect of proximity to these vegetation classes on seedling density (effective dispersal). At other sites, studies indicate that isolated trees (Willson and Crome 1989, Guevera et al. 1992), large monocots (Duncan and Chapman 1999), and shrub species (Vieira et al. 1994, Nepstad et al. 1996, Holl 2002) act as recruitment foci for tropical tree seedlings at abandoned sites by attracting seed dispersers. Studies also indicate that abiotic conditions in plots below remnant vegetation are superior for woody seedling growth and survival compared to grass-dominated sites (Guevera et al. 1992, Vieira et al. 1994, Nepstad et al. 1996, Holl 2002). Further research will be needed to determine whether increased seed dispersal, favorable growing conditions,

or a combination of the two is responsible for the elevated numbers of seedlings we record in close proximity to forest and remnant vegetation, in comparison to *Saccharum*-dominated sites. However, evidence for both is presented in associated studies. In an unpublished manuscript by E. Hooper, P. Legendre, and R. Condit, we document how insufficient seed dispersal, especially of large-seeded shade-tolerant species, limits their regeneration in the *Saccharum*. We also report increased germination, survival, and growth of most tree species planted in shaded, *Saccharum*-free plots as compared to *Saccharum*-dominated plots (Hooper et al. 2002). As shading eliminates the *Saccharum* while enhancing the performance of most tree species (Hooper et al. 2002), this suggests that planting trees to overcome dispersal limitations and produce a shade cover is the best way to eliminate the *Saccharum*. Once trees are established, they may act as regeneration nuclei by attracting seed dispersers and providing favorable growing conditions, thereby accelerating natural regeneration (Nepstad et al. 1990, Lamb et al. 1997).

The amount of time elapsing since the last fire also has significant impacts upon species composition. We differentiated time since fire at the site level and found that distinct patterns of species abundances at different distances from the forest depend upon site. Purata (1986) similarly reports that the interaction of time since disturbance and distance to the forest was important in determining floristic composition in abandoned Mexican fields. The relative importance of distance from the forest and distance from different remnant vegetation on species composition at our sites changes as time since fire increases. Distance from the forest significantly affects species composition 1 and 2 yr postfire, but not 3 and 4 yr postfire; as time since fire increases, distance from the remnant vegetation becomes more important. One year after fire, community composition of tree seedling regeneration is dominated by light-demanding, wind-dispersed species, with some small-bird-dispersed species present; their abundance declines exponentially with increasing distance from the forest; this decline is steep enough that few individuals are found 35 m from the forest. Similar results are reported by Aide and Cavelier (1994) in Columbian abandoned pastures; they found most woody species within 2 m from the forest edge. These results suggest that if abandoned areas are large, distance to the nearest seed source will limit the speed and species composition of natural forest regeneration; similar results are reported by Uhl et al. (1988) and Cubiña and Aide (2001). In contrast to sites close to the forest, the density of the bat-dispersed *Piper marginatum* increases with distance from the forest, peaking at 35 m and dominating the community there. At other neotropical sites, bats have a similar effect on tree regeneration because they disperse more seeds to locations farther from perches than birds (Gorchov et al. 1993, Cardosa da Silva et al. 1996, Medellin and

Gaona 1999). At distances furthest from the forest, few individuals are found except for species that can recruit from seed after fire (*Trema micrantha*) or are able to reproduce in these *Saccharum* grasslands (*Cochlospermum vitifolium*). Few individuals of large-arboreal-animal-dispersed species regenerate, and no large monocots, trees, saplings, or shrubs are present one year after fire. In contrast, as time since fire increases, naturally regenerating wind-dispersed species become progressively less abundant, large-animal-dispersed species become more abundant, and remnant vegetation becomes established, reaching a height great enough to overtop the *Saccharum*. The importance of distance from the forest on seedling community composition declines, while the importance of the remnant vegetation increases. Two years post-fire, significant differences in species composition result from the interaction of distance to remnant vegetation and forest; however, remnant vegetation has a more striking impact. For example, at one site, plots at both 10 and 85 m from the forest have similar community composition because both are adjacent to large monocots and remnant trees, whereas the species composition at 35 m is significantly different because no remnant vegetation is present there. Three and four years postfire, distance from the forest has no significant impact upon seedling community composition. In contrast, seedling density in plots with large monocots present is significantly higher than when they are absent (E. Hooper, P. Legendre, and R. Condit, *unpublished manuscript*); distance from the large monocots accounts for a high percentage (56.6%) of the total variation in seedling density. Significantly more species are found near large monocots as compared to *Saccharum*-dominated plots, underscoring the importance of remnant vegetation for increasing diversity during succession in these anthropogenic grasslands.

Successional interpretation

The chronosequence we record at our site differs from the general neotropical secondary successional model proposed by Finegan (1996), while at sites in close proximity to ours (<4 km) on Barro Colorado Island (BCI) that are not invaded by *Saccharum spontaneum*, successional trajectories generally follow Finegan's (1996) model. For example, Kenoyer (1929) reports a four-stage, post-disturbance succession on BCI: (1) grasses and weedy plants, replaced after a year by large monocots (*Heliconia* spp.) and shrubs of the genus *Piper*; (2) dominance by short-lived pioneers; (3) mixed secondary forest of longer-lived pioneers; (4) climax forest stage. We similarly record a dominance of the site by grasses (*Saccharum*) and clumps of large monocots in association with *Piper* species. Species from the short-lived pioneer stage are almost absent, however, while we record long-lived pioneer species that persist in mature forest. This suggests that species participating in succession become established

soon after site initiation, as proposed by Egler (1954). We characterize the species composition of these successional stages in turn.

Stage two (short-lived pioneers).—Kenoyer (1929) records dominance by short-lived pioneers of the genera *Cecropia*, *Trema*, and *Ochroma* for the third to 15th year following disturbance. In *Saccharum*-dominated sites, this phase is virtually absent. We record a significant decline in light-demanding species with time since fire, suggesting that pioneer species do not persist in these *Saccharum* grasslands. This could result from a combination of decreased seed bank viability and an inability of seedlings to compete with *Saccharum spontaneum*; indirect evidence suggests the former is important, while we present direct evidence for the latter. A comparison of our results with those of authors who studied seed bank dynamics near our site (<4 km) suggests that some potential pioneer species, especially those from the core pioneer genus *Cecropia*, have low seed bank viability at our site. For example, Dalling et al. (1998*a*) record very high densities of *Cecropia* spp. in the seed bank, while we found low germination of *Cecropia*, especially after fire. Similarly, at Amazonian sites, *Cecropia* species dominate the seed bank and the seedling communities regenerating after disturbance; however, if fire is present *Cecropia* species are extinguished as a component of the regeneration (Didham and Lawton 1999, Mesquita et al. 2001). Interestingly, *Cecropia* does persist at our sites near large monocots, which act as a green firebreak. The small-seeded pioneers that survive in the seed bank and germinate following fire (mainly *Trema micrantha*) have poor survival and therefore do not persist in the *Saccharum* because of competition with the *Saccharum*. In a companion study, we present direct evidence that small-seeded pioneer species have very low performance in the *Saccharum* because they can tolerate neither aboveground nor below-ground *Saccharum* competition (Hooper et al. 2002).

Stage three (long-lived pioneers).—Many of the species we record regenerating 1–4 yr after fire are those characteristic of the third stage of succession. Kenoyer (1929) records dominance by long-lived pioneers of the genera *Luehea*, *Apeiba*, *Miconia*, and *Cordia* in this third stage of succession, with shorter-statured trees and shrubs and in some places stands of *Gustavia superba* below their canopy; we similarly report a prevalence of these species. At 60-yr-old successional plots on Barro Colorado Island, Lang and Knight (1983) also report dominance by *Cordia alliodora* and *Luehea seemanii*, with *Gustavia superba* as the most abundant mid-canopy tree. We similarly record the presence of many of these species (34% species similarity) and dominance by *Gustavia superba*. The similarity of species composition between seedlings in our plots and those documented in 15–200 yr successional plots on BCI (Knight 1975) is also high; over 60% of the individuals and 31 species we record are also present in these third-phase successional plots on BCI, especially those from later successional plots. Thirteen of the species from our sites are present in the 15th year of succession, 29 are present in 50–80th year, and 27 are found in the 200th year plots of Knight (1975). Our data thus support the hypothesis of Finegan (1996) that regeneration of the long-lived pioneers is abundant in the first years of succession, and it also supports Egler's initial floristic composition model of succession (Egler 1954).

Stage four (mature forest).—Finegan (1996) and Kenoyer (1929) classify a fourth stage of succession as mature forest dominated by shade-tolerant species. Finegan (1996) states that the long-lived pioneers characteristic of the third phase are scarce in mature forests and therefore these two forest types are dominated by different taxa. We do not dispute that late successional and mature forest community composition is different; however, our data suggest that many species that colonize early in succession persist in mature tropical forest. For example, 54 of the 80 species we record regenerating are also components of the 50-ha plot of mature forest on BCI (Condit et al. 1996). These species represent 35.8% of all stems >10 mm dbh and 29.3% of all stems >100 mm dbh recorded in 1990 in the 50-ha plot on BCI; these species include long-lived pioneers, as well as mid- and understory species. Other researchers working near our site report similar findings. Denslow and Guzman (2000) also compare successional plots near ours with data from mature forest on BCI and report that primary forest species accumulate rapidly in the first few years after disturbance if propagule sources are close by. Knight (1975) found that all the canopy emergents in mature forest on BCI are long-lived pioneers (characterized as infrequently reproducing in the understory of mature forest). Milton et al. (1994) similarly document large individuals of heliophilic species in old-growth stands on BCI and suggest that these species have the potential to outlive many of the shade-tolerant species and persist for thousands of years.

These results suggest that elements of both the general model of neotropical succession proposed by Finegan (1996) and based on the initial floristics model (Egler 1954) as well as the nucleation model of Yarranton and Morrison (1974) are applicable in *Saccharum*-dominated abandoned agricultural lands in Panama. Our data show that time since fire significantly affects species composition, with light-demanding medium-sized trees present significantly more often in early postfire communities and shade-tolerant understory species present significantly more often as time since fire increases, as predicted by the successional model of Finegan (1996). However, we also find that the presence of regenerating tree species with different dispersal mechanisms changes with time since fire; wind-dispersed species are present significantly more often in early post-fire communities while large-arboreal-an-

imal-dispersed species are present significantly more often as time since fire increases. The spatial distribution of naturally regenerating tree species is significantly and positively affected by proximity to the forest and remnant vegetation, with the species composition of the regeneration significantly affected by the identity of the vegetation (ex-forest, large monocot) found in close proximity; these results follow the nucleation model of Yarranton and Morrison (1974). Therefore, while species composition is similar to the third stage, and many species persist into the mature forest stage of the general neotropical successional model of Finegan (1996), the spatial distribution of these species follows the nucleation model of succession, where naturally regenerating forest species are distributed in close proximity to forest and remnant vegetation present in the grasslands. Our results suggest that recruitment limitation is the main determinant of species composition, as has been suggested for mature forest composition on BCI (Hubbell et al. 1999). These results corroborate the statement of Finegan (1984, 1996) that a deterministic concept of succession cannot be the whole explanation for species composition at a site. Deterministic successional models suggest that species compositional sequence results from competition between species with different life histories and competitive abilities establishing at or shortly after site disturbance. These models do not take into account the nature of seed dispersal or the filtering effect of initial site conditions on propagule dispersal, seedling establishment, and survival. Williams et al. (1969) highlight the importance of incorporating spatial factors in successional models, reporting that floristic composition changed from a temporal to a spatial organization after a year following clearing of Queensland rain forest. We also find that temporal and spatial factors affect the species composition of forest succession in deforested and abandoned lands invaded by *Saccharum spontaneum*; both must be considered for a complete description of succession.

Fire, however, sets back succession in these highly flammable *Saccharum*-dominated grasslands; in the continual presence of fire, the successional sequence documented at our sites is unlikely to proceed very far, and a *Saccharum*-dominated grassland will continue to effectively preclude woody species regeneration. Similar results of grass invasion are reported for the Brazilian Amazon where repeatedly burned lands are dominated initially by grasses, potentially suppressing the recruitment of tree seedlings for years (Cochrane and Schulze 1998). Grasses maintain a fire regime which, in the worst cases, permanently deflects succession to a savanna and scrub vegetation (D'Antonio and Vitousek 1992); this could lead to the impoverishment of vast expanses of tropical lands (Uhl 1998), as has been reported in much of the Old World tropics. For example, Otsamo et al. (1995) report that in Indonesia alone 64×10^6 ha of previously forested land are dom-inated by *Imperata cylindrica* and *Saccharum spontaneum* grasslands, as a result of repeated logging and fire. Low-diversity, fire-maintained species communities may result, as we found at our *Saccharum*-dominated sites. Resprouting species form the majority of individuals rebounding initially after fire (51% of individuals present initially after fire are resprouts, as compared to 31% of individuals present at sites unburned for at least 2 yr). However, only a few dominant species resprout after fire while many more species resprout less frequently, if at all. Therefore, in Panama, as at sites in the Amazon (Miller and Kauffman 1998), the inability to resprout can result in local species extinction when seed dispersal is limited, and the seed bank becomes degraded, impoverishing the biodiversity of forest regeneration. Our data show that this threat to forest regeneration is now present in Panama, wherever *Saccharum spontaneum* is present.

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APPENDIX A

Details of the statistical methods utilized in the paper are available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A1.

APPENDIX B

A diagram of the experimental design is available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A2.

APPENDIX C

A table of species characteristics and abundances of all species naturally regenerating in *Saccharum*-dominated grasslands is available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A3.

APPENDIX D

Results of nonlinear regression analyses modeling the effect of distance from the various classes of remnant vegetation and abiotic factors on the density of naturally regenerating tree and shrub species are available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A4.

APPENDIX E

Results of fourth-corner correlation analyses comparing dispersal vector with time since fire are available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A5.

APPENDIX F

Results of fourth-corner correlation analyses comparing species characteristics with time since fire and distance from the forest are available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A6.

APPENDIX G

Results of fourth-corner correlation analyses comparing adult size of individuals regenerating in the *Saccharum*-dominated grasslands with time since fire are available in ESA's Electronic Data Archive: *Ecological Archives* E085-116-A7.

APPENDIX A

Ecological Archives **E085-116-A1**

DETAILS OF THE STATISTICAL METHODS

INTRODUCTION

We utilized multivariate methods to determine the effect of the experimental factors distance from the forest, *Saccharum* competition, time and fire on species composition; in a companion paper, we investigated their effects on the density and diversity of tree species recruitment (Hooper et al. in review). While multivariate analyses have been successfully used in studies of tropical succession to distinguish temporal trends from environmental patterns and randomness and to estimate successional vectors of species composition (for example, see Healey and Gara 2003, Mesquita et al. 2001, Aide et al. 2000, Sheil 1999, Aide et al. 1996, Purata 1986, Knight 1975, Williams et al. 1969), multivariate approaches have been criticized because they are often merely descriptive instead of experimental and thus have not increased our ability for prediction or control of succession (Austin 1977). Distance measures utilized in conventional ordination analyses are often not appropriate for tropical data which is characterized by the presence of a high number of rare species. To address these issues, we used an experimental approach and were able to assess the significance of our experimental factors in determining species composition through the use of a recently developed method, distance-based redundancy analysis (db-RDA, Legendre and Anderson 1999). This method is advantageous because it allowed us to use distance measures appropriate in the presence of a high number of rare species. We used 4th corner analysis, another recently-developed method, to correlate the species attributes associated with successional stages (Legendre et al. 1997) and test the significance of these correlations.

We relate our results to previous tropical successional hypotheses, namely the initial floristic composition model (applied to tropical succession by Finegan 1996) and the nucleation model (Yarranton and Morrison 1974). To evaluate the importance of succession following the nucleation model, we determined the effect of trees, shrubs and large-leaved monocots on natural tree regeneration by documenting their locations and measuring their proximity to each naturally-regenerating seedling. We used a chronosequence, or space-for-time substitution approach, by studying floristic composition on plots at sites with known time since disturbance (fire). We separated the effects of spatial and temporal variation by using contiguous plots at replicated sites, as recommended by Austin (1977), coupled with appropriate analyses designed to test separately for the effects of site and temporal trend; this separation is important in successional studies utilizing a space-for-time substitution approach (Williams et al. 1969, Austin 1977, Swaine and Greig Smith 1980). To ensure that the successional trend occupied more variance than the within-year differences (Legendre et al. 1985), we separated the effects of short- and long-term variation by using repeated measurements from the same plots over a year (short-term variation) and comparing this to the effect of time-since-fire at each site (long-term variation).

PROBLEMS WITH USE OF CONVENTIONAL MULTIVARIATE ANALYSES

A major problem with the use of multivariate techniques for studying secondary succession of tropical rainforest is the choice of an appropriate distance measure for simple or canonical

ordination analysis. Species abundance data in the tropics often produce matrices (sites x species) characterized by the presence of many rare species, each of which is found in very few plots. For this type of data, the Euclidean distance measure preserved in principal component analysis (PCA) and canonical redundancy analysis (RDA) is inappropriate (Legendre and Legendre 1998, Legendre and Gallagher 2001). Correspondence analysis and its canonical form, CCA, utilize an appropriate distance measure for analyzing data with unimodal response curves and double-zeros. However they overemphasize rare species; therefore, ecological decisions using the results of these methods will be based on the characteristics of the rare species. Nonmetric multidimensional scaling and principal coordinate analysis (PCoA) are not canonical ordination methods. Therefore most of the classical multivariate methods are problematic for characterizing secondary tropical succession.

JUSTIFICATION FOR OUR USE OF DISTANCE-BASED REDUNDANCY ANALYSIS (db-RDA)

We needed to test the results of field experiments, using community composition as the multivariate response variable. MANOVA cannot be used with this data because it violates the assumption of multivariate normality and homogeneity of within-group covariance matrices. As well, MANOVA cannot be used when the number of species is greater than the number of sites, as was the case in our study where we recorded 80 species at 45 sites. We could not use non-parametric statistical methods, such as the Mantel test, because they do not allow tests of multivariate interactions between factors in an ANOVA design. Distance-based redundancy analysis (db-RDA) provides a solution for data such as ours (Legendre and Anderson 1999). Db-RDA provides the flexibility of choosing a distance measure which is appropriate for community composition data containing a high number of rare species; it allows for testing the main factors as well as the interaction terms of an ANOVA model; it uses permutation testing which does not require multivariate normality; it can be used with response data containing more species than there are sites; and it allows users to draw biplots to represent the ANOVA results.

DETAILS OF METHODOLOGY

I. Effect of distance from the forest, Saccharum *competition, time, site and fire on community composition.*—Distance-based redundancy analysis (db-RDA) was used to test the significance of these experimental factors and their interaction terms in an ANOVA model, using species assemblage (a table of species abundances by subplots) as the response variable. Details of the procedure are outlined in Legendre and Anderson (1999). The experimental factors of distance from the forest, treatment of the *Saccharum spontaneum*, site, fire, and time were coded as orthogonal dummy variables. The effect of all five experimental factors could not be analyzed in a single analysis; different data were needed to test for time, site and fire (Table A1). We therefore analyzed our data using db-RDA with various three-way ANOVA designs: (1) To test for the effect of time, distance from the forest, *Saccharum* competition, and their interactions, data from all four time periods at the three sites that were not burned by wildfire, or by prescribed burn, were utilized (108 subplots). (2) To test for the effect of site, distance from the forest, and *Saccharum* competition, only the December 1996 data could be used because site replication was achieved by using the data collected before the prescribed burn on both sides of the firebreak at each site (90 subplots). (3) To test for the effect of fire, we used two response variable data tables: (A) burned vs. unburned. This was done as the experiment was originally planned, comparing the data collected in the final census in the burned (prescribed burn) and unburned sides of the two sites that received a prescribed burn and escaped uncontrolled fires

(36 subplots). Because of this lack of power, we also conducted an alternative analysis (B) and compared before vs. after the burn on all plots that were burned regardless of whether it was as a result of wild or prescribed fires (108 subplots). The response data tables in all analyses included total number of individuals per species and number of recruits per species. Two additional response tables were also utilized for the fire analyses: total number of root sprouts per species, and a combined data table of the total number of root sprouts and recruits per species. The latter analysis is used to differentiate the effect of fire on the two mechanisms of regeneration in a single analysis; it treats the same species with two origins (root sprout and recruit) as if they were two different species. To de-emphasize rare species, this final analysis was performed using only those species where 10 or more individuals had been recorded.

Redundancy analysis (RDA) was applied to the set of all principal coordinates (PCoA, Gower 1966) derived from the Bray-Curtis distance matrix among sites to test the significance of the main factors and the interactions. We used the Bray-Curtis distance measure within the db-RDA analyses because it does not give disproportionate weight to rare species (Legendre and Legendre 1998). The principal coordinates were corrected for negative eigenvalues using the Lingoes method (Gower and Legendre 1986, Legendre and Anderson 1999).

A special procedure was utilized for biplot representation, because the identity of the original species is lost when principal coordinates are computed from the Bray-Curtis distance matrix in the db-RDA procedure. The original species data were transformed using the chord transformation described by Legendre and Gallagher (2001), chosen because it does not give disproportionate weight to the rare species. The transformed data table was analyzed using RDA and utilized to produce ordination biplots. To further de-emphasize rare species, only those species represented by 5 or more individuals were represented in the biplots.

TABLE A1. Data matrices used in the 10 three-way db-RDA analyses. Response = response variables: Total = all data; Recruits; Rootsprouts; Rootsprouts and recruits = rootsprouts and recruits included in this analysis, but coded differently for each species. + = unburned plots, * = burned plots.

Factors tested	Response	Aug. 96	Dec. 96	April 97	Aug. 97
Time, distance, treatment	Total	+	+	+	+
Time, distance, treatment	Recruits	+	+	+	+
Site, distance, treatment	Total		+		
Site, distance, treatment	Recruits		+		
Fire, distance, treatment	Total		+		*
Fire, distance, treatment	Recruits		+		*
Fire, distance, treatment	Rootsprouts		+		*
Fire, distance, treatment	Rootsprouts and recruits		+		*
Fire, distance, treatment	Total				*, +
Fire, distance, treatment	Recruits				*, +

   II. Effect of time since fire.—To test the significance of time since fire on species composition, and relate it to our experimental factors (distance from the forest and *Saccharum* treatment), forward selection of the (ln + 0.01)-transformed environmental variables (time since fire, distance from the forest, and both live and dead *Saccharum* biomass) was performed using RDA. This was carried out on the species matrix of number of individuals (chord-transformed) recorded per site in December 1996. A Monte-Carlo permutation test with 999 permutations was used to assess the statistical significance of each variable, as was the case for all multivariate analyses we utilized.

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APPENDIX B

Ecological Archives **E085-116-A2**

DIAGRAM OF THE EXPERIMENTAL DESIGN
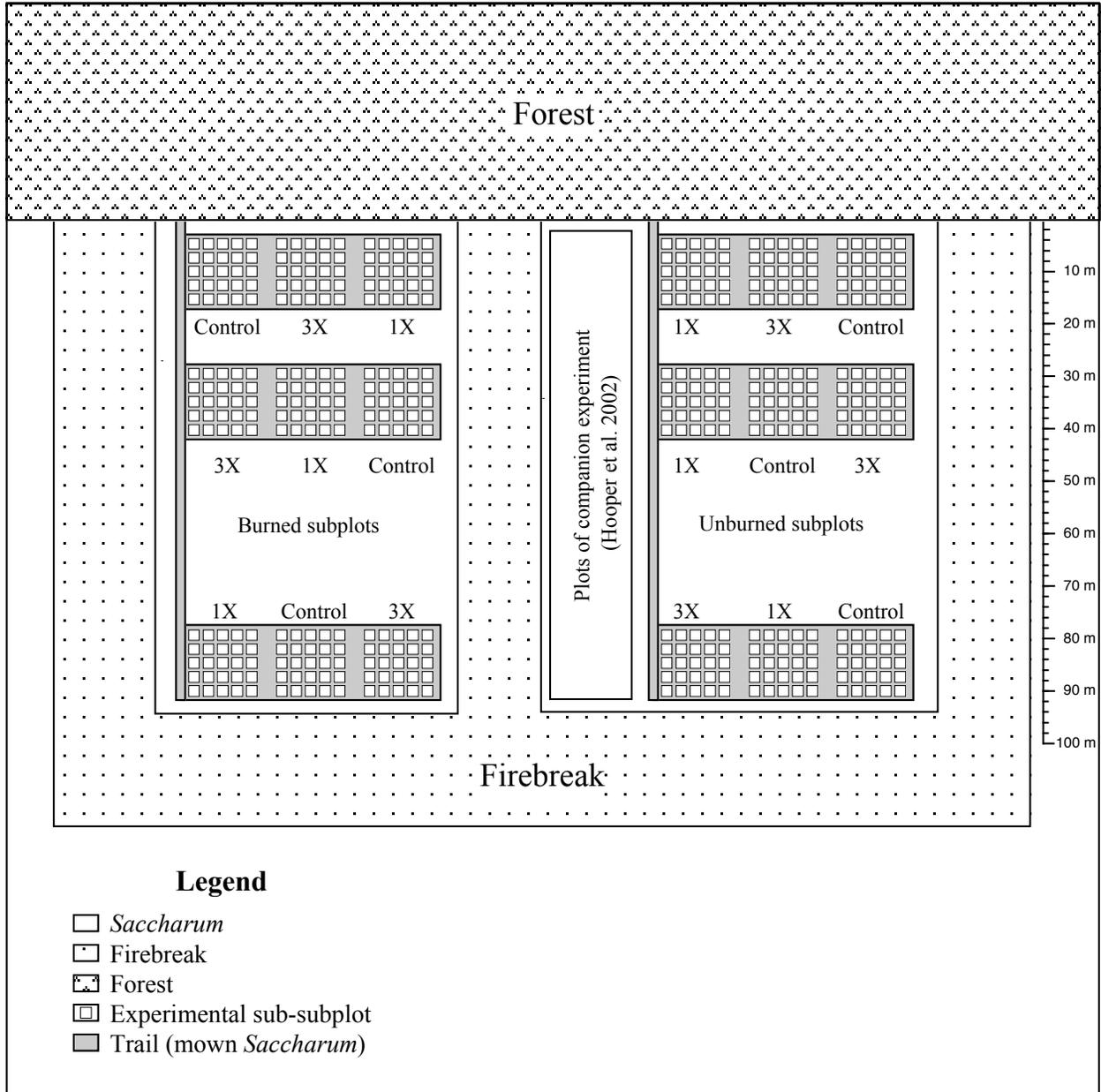
FIG. B1. Diagram of experimental design showing a hypothetical plot with associated burned and unburned sections, and mowing treatments of the *Saccharum* (1x, 3x, control).

APPENDIX C

***Ecological Archives* E085-116-A3**

SPECIES CHARACTERISTICS AND ABUNDANCES OF ALL SPECIES
NATURALLY REGENERATING IN *SACCHARUM*-DOMINATED GRASSLANDS

TABLE C1. Species characteristics of all naturally-regenerating species recorded: species name, family, total number of individuals recorded during the entire regeneration experiment not including root sprouts (NR), total number of individuals recorded during the entire experiment including root sprouts (All), growth form of adult (F), shade-tolerance category (L), seed size category (S), and dispersal mechanism or vector (Dispersal).

Species	Family	NR	All	F[§]	L[ʃ]	S[£]	Dispersal[¥]
Acalypha diversifolia	Euphorbiaceae	28	29	S	G	1	ballistic
Acalypha macrostachya	Euphorbiaceae	1	1	U		1	ballistic
Adelia triloba	Euphorbiaceae	5	5	U	G	1	ballistic
Alibertula edulis	Rubiaceae	5	5	U	S	3	large animal
Alseis blackiana	Rubiaceae	6	9	T	S	1	wind
Anacardium excelsum	Anacardiaceae	1	1	T		3	large animal
Anacardium occidentale	Anacardiaceae	3	7			3	large animal
Annona hayessii	Annonaceae	3	3			1	small birds
Annona spraguei	Annonaceae	6	11	M	P	1	small birds
Apeiba membranaceae	Tiliaceae	8	8	T		1	large animal
Apeiba tibourbou	Tiliaceae	34	34	M		1	large animal
Ardisia revoluta	Myrsinaceae	14	15		G	1	small birds
Banara guianensis	Flacourtiaceae	66	181		G	1	small birds
Brosimum alicastrum	Moraceae	4	5	T	S	2	large animal
Byrsonima crassifolia	Malpighiaceae	193	196		P	3	large animal
Carica papaya *	Caricaceae	2	2				
Cassia moschata	L: Caesalpinioideae	4	7		S	2	
Casearia arguta	Flacourtiaceae	9	18		G	1	small birds
Casearia commersoniana	Flacourtiaceae	10	40		G	1	small birds
Cecropia insignis	Moraceae	236	237	T	P	1	small birds
Cnestidium rufescens *	Connaraceae	1	2				
Coccoloba manzanillensis	Polygonaceae	2	2	U	S	1	
Cochlospermum vitifolium	Cochlospermaceae	243	400		P	1	wind
Colubrina glandulosa	Rhamnaceae	2	4			1	ballistic
Connarus panamensis	Connaraceae	1	2				
Cordia alliodora	Boraginaceae	73	241	T	G	1	wind
Cordia bicolor	Boraginaceae	9	61	T	G	2	large animal
Cordia porcata	Boraginaceae	1	1				
Croton billbergianus	Euphorbiaceae	40	40	U	P	1	ballistic
Didymopanax morototoni	Araliaceae	3	3			1	small birds
Ficus (species unknown)	Moraceae	3	8			1	small birds

TABLE C1 (continued)

Species	Family	NR	All	F§	L♩	S£	Dispersal¥
Flemingia strobilfera *	L: Papilionoideae	2	2				
Gustavia superba	Lecythidaceae	679	1060	M	G	3	agouti
Hamelia patens	Rubiaceae	1	1			1	small birds
Hampea appendiculata	Malvaceae	1	1	M	G	2	small birds
Heliocarpus americanus	Tiliaceae	1	1			2	
Herrania purpurea	Sterculiaceae	5	12	U	G	2	
Hura crepitans	Euphorbiaceae	1	1	T		2	ballistic
Hybanthus prunifolius	Violaceae	57	141	S	S	1	ballistic
Inga sapindoides	L: Mimosoideae	2	3	M	G	2	large animal
Inga vera	L: Mimosoideae	83	182		G	3	large animal
Jacaranda copaia	Bignoniaceae	4	4	T		1	wind
Lonchocarpus latifolius	L: Papilionoideae	2	17	T	S	3	large animal
Luehea seemannii	Tiliaceae	21	21	T	G	1	wind
Mangifera indica *	Anacardiaceae	1	1				
Margaritaria nobilis	Euphorbiaceae	3	6			1	small birds
Miconia argentea	Melastomataceae	68	68	M	P	1	small birds
Ochroma pyramidale	Bombacaceae	15	15		P	1	wind
Ocotea (species unknown)	Lauraceae	1	1				small birds
Ouratea lucens	Ochnaceae	1	2	S	S	1	
Piper marginatum	Piperaceae	500	522		G	1	bats
Pithocellobium barbourianum	L: Mimosoideae	1	1			2	large animal
Platymiscium pinnatum	L: Papilionoideae	6	19	T	S	3	large animal
Posoqueria latifolia	Rubiaceae	6	9	M	S	2	large animal
Protium panamense	Burseraceae	1	1	M	S	2	large animal
Pseudobombax septenatum	Bombacaceae	7	20	T		1	wind
Psychotria grandis	Rubiaceae	34	40	U	G	1	small birds
Psychotria luxurians	Rubiaceae	2	2				
Quassia amara	Simaroubaceae	20	121	U	G	2	large animal
Randia formosa	Rubiaceae		1	1			large animal
Senna dariensis	L: Caesalpinioideae	4	7	S	G		
Solanum hayesii	Solanaceae	84	125	M	G	1	small birds
Sorocea affinis	Moraceae	1	3		S	1	
Spondias mombin	Anacardiaceae	214	290	T	P	3	large animal
Stemmadenia grandiflora	Apocynaceae	4	18			1	
Sterculia apetala	Sterculiaceae	1	2		G	3	large animal
Swartzia simplex (*grandiflora*)	L: Caesalpinioideae	8	30	U	S	3	large animal
Swartzia simplex (*ochnacea*)	L: Caesalpinioideae	56	158	U	S	3	large animals
Tabebuia guayacan	Bignoniaceae	9	30	T	S	1	wind
Tabebuia rosea	Bignoniaceae	1	1	T	S	2	wind
Thevetia ahouai	Apocynaceae	45	74	U	S	1	small birds
Trema micrantha	Ulmaceae	161	161		G	1	small birds

TABLE C1 (continued)

Species	Family	NR	All	F[§]	L[⅃]	S[£]	Dispersal[¥]
Trichilia tuberculata	Meliaceae	6	6	T	S	2	small birds
Trichospermum galeotti	Tiliaceae	171	174		G	1	wind
Trophis racemosa	Moraceae	18	21	M	S	1	small birds
Turnera panamensis	Turneraceae	1	2			1	small birds
Vatairea erythrocarpa	L: Papilionoideae	6	7			3	
Vernonia patens	Compositae	2	2		G	1	
Vismia macrophylla	Clusiaceae	12	17			1	small birds
Xylopia frutescens	Annonaceae	3	3			1	small birds

Notes:
* Introduced species
L: Leguminosae
[§] T = large tree, M = medium tree, U = treelet, S = shrub (from Condit et al. 1995)
[⅃] Shade tolerance categories: P = pioneer (light index > 3.0), G = gap species (light index 0–3.0), S = shade-tolerant species (light index less than 0). Light indices are from Condit et al. (1996) and Hooper et al. (2002)
[⅃] Seed size classes: $1 \leq 1$ cm; $2 = 1$–2 cm; $3 \geq 2$ cm (from Croat 1978)
[¥] Based on observations at BCI, 4 km from our site (R. Perez and R. Foster, pers. comm.)

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<center>**APPENDIX D**</center>

<center>*Ecological Archives* **E085-116-A4**</center>

<center>NONLINEAR REGRESSION ANALYSES MODELING THE EFFECT OF DISTANCE FROM THE VARIOUS CLASSES OF REMNANT VEGETATION AND ABIOTIC FACTORS ON THE DENSITY OF NATURALLY-REGENERATING TREE AND SHRUB SPECIES</center>

TABLE D1. Summary of results of nonlinear regression analyses modeling the effect of distance from the various classes of remnant vegetation (biotic) and abiotic factors on the density of naturally-regenerating tree and shrub species per 10 m^2. Only the variables that were significant ($P < 0.05$) following backward elimination are presented. For remnant vegetation classes, both the negative exponential (Ex) and linear functions (Lin) were used in the model. All reported values in the 10 left-hand columns are R^2 statistics resulting from regression against a single explanatory variable of distance from the various remnant vegetation classes or abiotic factors. Positive exponent: increasing density with distance from source; negative exponent: decreasing density with distance from source. Source includes: distance from the forest (Forest), distance from the nearest large-leaved monocot (Monocot), distance from the nearest remnant tree larger than 5 m in height (Tree), and distance from the nearest shrub or sapling 2.5–5 m in height (Shrub). Habitat: see note[®]. Biotic = partial R^2 for all biotic variables. Abiotic = partial R^2 for all abiotic variables. Total = total R^2 for the (multiple) nonlinear regression model. $F = F$ statistic; $n = 90$.

Species[§]	Forest Ex	Forest Lin[ᶷ]	Monocot Ex	Monocot Lin[£]	Tree Ex	Tree Lin[¥]	Shrub Ex	Shrub Lin[ȼ]	Habitat[®] linear	Habitat linear	Biotic partial	Abiotic partial	Total	F	P
Total density of all individuals															
	–	–	0.566⁻	–	–	–	–	–	–	–	0.566	0.000	0.566	$F_{[3,87]}=22.65$	<0.0001
Total number of species															
	–	0.611⁻	0.662⁻	–	–	–	–	–	–	–	0.679	0.000	0.679	$F_{[4,86]}=7.24$	0.0002
1. Wind-dispersed species (not reproducing)															
Tric ga	–	0.091⁻	–	–	–	–	–	–	Fire 0.108⁻	–	0.091	0.108	0.161	$F_{[3,87]}=6.15$	0.0032
Lueh se	–	0.133⁻	–	–	–	–	–	–	–	–	0.133	0.000	0.133	$F_{[2,88]}=6.80$	0.0107
Cord al	–	–	–	–	–	–	–	–	Fire 0.164⁺	–	0.000	0.164	0.164	$F_{[1,89]}=17.47$	<0.0001
2. Wind-dispersed species (reproducing)															
Coch vi	–	–	–	–	–	–	–	–	Fire 0.111⁻ Dead 0.120⁻		0.000	0.171	0.171	$F_{[3,87]}=4.49$	0.0139
3. Ballistic-dispersed species															
Hyba pr	–	0.113⁻	0.335⁻	–	–	0.155⁻	–	–	–	–	0.464	0.000	0.464	$F_{[5,85]}=15.85$	<0.0001

TABLE D1 (continued)

Species[§]	Forest Ex	Forest Lin[⁹]	Monocot Ex	Monocot Lin[£]	Tree Ex	Tree Lin[¥]	Shrub Ex	Shrub Lin[ᶜ]	Habitat[®] linear	Habitat[®] linear	Biotic partial	Abiotic partial	Total	F	P
4. Small-bird-dispersed species															
Mico ar	–	–	–	–	0.173⁻	–	–	–	–	–	0.173	0.000	0.173	$F_{[2,88]}=9.21$	0.0002
Cecr in	–	–	0.312⁻	–	–	0.168⁺	–	–	–	–	0.440	0.00	0.440	$F_{[6,84]}=12.03$	<0.0001
Bana gu	–	–	–	–	–	–	–	–	–	–	0.000	0.000	0.000		
Trem mi	–	–	–	–	–	–	–	–	–	–	0.000	0.000	0.000		
Psyc gr	–	–	–	–	0.147⁻	–	–	–	–	–	0.147	0.000	0.147	$F_{[2,88]}=7.59$	0.0009
5. Bat-dispersed species															
Pipe ma	–	–	0.577⁻	–	–	–	–	–	–	–	0.577	0.000	0.577	$F_{[3,87]}=47.97$	<0.0001
6. Large-arboreal-animal-dispersed species															
Thev ah	–	0.096⁻	–	–	–	–	–	–	–	–	0.096	0.000	0.096	$F_{[2,88]}=4.50$	0.0368
Quas am	–	–	–	–	–	–	–	–	–	–	0.000	0.000	0.000		
Byrs cr	–	–	–	–	–	–	–	0.112⁻	–	–	0.112	0.000	0.112	$F_{[2,88]}=5.18$	0.0252
Swar s2	–	0.250⁺	–	–	–	–	–	–	Dead 0.284⁺	–	0.250	0.284	0.317	$F_{[3,87]}=6.48$	0.0024
Inga ve	–	0.223⁻	–	–	–	–	–	–	–	–	0.223	0.000	0.223	$F_{[2,88]}=4.76$	0.0318
Spon mo	–	–	–	–	–	–	–	–	–	–	0.000	0.000	0.000		
7. Agouti-dispersed species															
Gust su	–	–	0.449⁻	–	–	–	–	–	Dead 0.283⁺	–	0.449	0.283	0.479	$F_{[4,86]}=17.73$	<0.0001

Notes:

[§] Species: Bana gu = *Banara guianensis*, Byrs cr = *Byrsonima crassifolia*, Cecr in = *Cecropia insignis*, Coch vi = *Cochlospermum vitifolium*, Cord al = *Cordia alliodora*, Gust su = *Gustavia superba*, Hyba pr = *Hybanthus prunifolius*, Inga ve = *Inga vera*, Lueh se = *Luehea seemannii*, Mico ar = *Miconia argentea*, Pipe ma = *Piper marginatum*, Psyc gr = *Psychotria grandis*, Quas am = *Quassia amara*, Spon mo = *Spondias mombin*, Swar s2 = *Swartzia simplex* var. *ochnacea*, Thev ah = *Thevetia ahouai*, Trem mi = *Trema micrantha*, Tric ga = *Trichospermum galeotti*

[⁹] Square root of distance from the forest

[£] Distance from the nearest large-leaved monocot (*Musa* sp., *Heliconia* sp.)

[¥] Square root of distance from the nearest isolated old-field tree larger than 5 m in height

[ᶜ] Ln(distance from the nearest shrub or sapling between 2.5 m and 5 m in height)

[®] Abiotic variables include: Live = biomass of live *Saccharum* (g), Dead = biomass of *Saccharum* litter (g), Fire = time since last wildfire (months). All abiotic variables were ln($x + 1$) transformed, except fire; time since the last wildfire was not transformed

APPENDIX E

Ecological Archives **E085-116-A5**

4$^{\text{TH}}$ CORNER CORRELATION ANALYSES
COMPARING DISPERSAL VECTOR WITH TIME SINCE FIRE

TABLE E1. Dispersal vector or mechanism (see text) compared to time since fire. The table reports fourth-corner correlation statistics $r(i,j)$, and probabilities (P) tested using 999 permutations followed by adjustment for multiple comparisons using Holm's procedure. **: $P < 0.01$.

	1.Wind, not reproducing	2.Wind, reproducing	3.Ballistic	4.Small birds	5.Bats	6.Large arboreal animals	7.Agouti	Resprout index[§]
$r(i,j)$	–0.0435	–0.1329	0.0806	–0.0390	–0.0380	0.1231	–0.0364	0.1382
P	0.5400	0.0080**	0.1200	0.5400	0.5400	0.0080**	0.5400	0.0080**

Note:
[§] Resprout index: number of individuals originating from root sprouts divided by the total number of individuals. It indicates the ability of a species to resprout.

APPENDIX F

Ecological Archives **E085-116-A6**

4TH CORNER CORRELATION ANALYSES COMPARING SPECIES CHARACTERISTICS
WITH TIME SINCE FIRE AND DISTANCE FROM THE FOREST

TABLE F1. Species characteristics, including light index, seed size, and resprout index, compared to time since fire and distance from the forest. The table reports fourth-corner correlation statistics $r(i,j)$ and probabilities (P) tested using 999 permutations followed by adjustment for multiple comparisons using Holm's procedure. *: $P < 0.05$; **: $P < 0.01$.

	Light index[§]	Seed size (mm)	Resprout index[ꟸ]
Time since fire (months)			
$r(i,j)$	–0.15507	0.04682	0.16238
P	0.00100**	0.08200	0.00100**
Distance from forest (m)			
$r(i,j)$	–0.04605	0.07187	0.03708
P	0.12600	0.02500*	0.17800

Notes:
[§] Light index was calculated in Condit et al. (1996). Species with a high light index (> 3.0) are pioneers and light demanding, those with a low light index (< 0) are shade tolerant, and those between 0 and 3.0 are gap-dependent.
[ꟸ] Resprout index (calculated as the number of individuals originating from root sprouts divided by the total number of individuals) indicates the ability of each species to resprout

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Condit, R., S. P. Hubbell, and R. B. Foster. 1996. Assessing the response of plant functional types to climatic change in tropical forests. Journal of Vegetation Science **7**: 405–416.

APPENDIX G

Ecological Archives **E085-116-A7**

4TH CORNER CORRELATION ANALYSES COMPARING ADULT SIZE OF INDIVIDUALS
REGENERATING IN THE *SACCHARUM*-DOMINATED GRASSLANDS WITH TIME SINCE FIRE

TABLE G1. Adult size of individuals, as defined in Condit et al. (1995), regenerating in the *Saccharum*-dominated grasslands, related to time since fire (months). The table reports fourth-corner correlation statistics $r(i,j)$ and probabilities (P) tested using 999 permutations followed by adjustment for multiple comparisons using Holm's procedure. *: $P < 0.05$; **: $P < 0.01$.

	Large tree	Mid-sized tree	Treelet	Shrub
$r(i,j)$	0.0711	–0.1842	0.0441	0.1201
P	0.0700	0.0040**	0.1560	0.0150*

LITERATURE CITED

Condit, R., S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of severe drought. Ecological Monographs **65**: 419–439.