Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape

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Abstract. Planting native tree seedlings is the predominant restoration strategy for accelerating forest succession on degraded lands. Planting tree "islands" is less costly and labor intensive than establishing larger plantations and simulates the nucleation process of succession. Assessing the role of island size in attracting seed dispersers, the potential of islands to expand through enhanced seed deposition, and the effect of planting arrangements on seed dispersal by birds and bats informs restoration design. Determining the relative importance of local restoration approach vs. landscape-level factors (amount of surrounding forest cover) helps prioritize methods and locations for restoration. We tested how three restoration approaches affect the arrival of forest seeds at 11 experimental sites spread across a gradient of surrounding forest cover in a 100-km^2 area of southern Costa Rica. Each site had three 50 × 50 m treatments: (1) control (natural regeneration), (2) island (planting tree seedlings in patches of three sizes: 16 m^2, 64 m^2, and 144 m^2), and (3) plantation (planting entire area). Four tree species were used in planting (*Terminalia amazonia*, *Vochysia guatemalensis*, *Erythrina poeppigiana*, and *Inga edulis*). Seed rain was measured for 18 months beginning ~2 years after planting.

Plantations received the most zoochorous tree seeds (266.1 ± 64.5 seeds·m^{-2}·yr^{-1} [mean ± SE]), islands were intermediate (210.4 ± 52.7 seeds·m^{-2}·yr^{-1}), and controls were lowest (87.1 ± 13.9 seeds·m^{-2}·yr^{-1}). Greater tree seed deposition in the plantations was due to birds (0.51 ± 0.18 seeds·m^{-2}·d^{-1}), not bats (0.07 ± 0.03 seeds·m^{-2}·d^{-1}). Seed rain was primarily small-seeded, early-successional species. Large and medium islands received twice as many zoochorous tree seeds as small islands and areas away from island edges, suggesting there is a minimum island size necessary to increase seed deposition and that seed rain outside of planted areas is strongly reduced. Planting design was more important for seed deposition than amount of forest cover within the surrounding 100- and 500-m radius areas. Establishing plantations and large islands facilitates the arrival of early-successional tree seeds and represents a broadly applicable strategy for increasing seed rain on abandoned agricultural lands. However, more intensive restoration approaches may be necessary for establishment of dispersal-limited species.

Key words: forest succession; nucleation; plantations; restoration; rural landscapes; seed dispersal; seed rain; tree islands; tropical montane forest.

Introduction

Tropical forest restoration is an important component of global strategies to conserve biodiversity and sequester atmospheric carbon, particularly in areas where forests have been extensively cleared and socio-economic forces are causing land to be removed from agricultural uses at large scales (Lamb et al. 2005, Wright and Muller-Landau 2006, Chazdon 2008). Natural recovery of tropical forests on abandoned and degraded agricultural lands can be limited by a range of factors beginning with severely restricted dispersal of forest seeds into cleared areas (e.g., Duncan and Chapman 1999, Holl 1999, Wijdeven and Kuzee 2000,

Rodrigues Da Silva and Matos 2006). The lack of seed dispersal by animals in particular is a major impediment to forest recovery because soil seed banks are rapidly depleted by intensive land uses such as grazing, tillage, and burning (Zimmerman et al. 2000, Cubina and Aide 2001), and animal-dispersed seeds decreases dramatically within only a few meters of forest edges (e.g., Gorchov et al. 1993, Holl 1999, Dosch et al. 2007). This limited dispersal is particularly problematic in wet tropical forest ecosystems where 60–90% of forest canopy trees and nearly 100% of shrubs and subcanopy trees are adapted for animal dispersal (Howe and Smallwood 1982).

Planting native tree seedlings in plantations is the predominant strategy for accelerating forest succession (Lamb et al. 2005, Chazdon 2008). Trees attract seed dispersing animals by providing perching and roosting sites, habitat for foraging, and cover from predators.

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Trees also facilitate movement of birds and bats through agricultural landscapes (McDonnell and Stiles 1983, Nepstad et al. 1991, Estrada et al. 1993, Guevara and Laborde 1993, Wunderle 1997, Harvey 2000b). In addition, trees serve to overcome a range of barriers to seedling establishment by shading out competitive grasses (Parrotta 1992, Guariguata et al. 1995), ameliorating microclimatic conditions (Guevara et al. 1992, Parrotta 1995, Holl 1999, Nepstad et al. 1999), and improving soil chemical and physical properties (Sanchez et al. 1985, Montagnini and Sancho 1994, Ashton et al. 1997). Establishing and maintaining plantations of trees, however, can be an expensive and labor-intensive endeavor. Accordingly, it is becoming increasingly important to develop strategies that are both ecologically and economically effective alternatives for restoring large areas of abandoned lands with limited available resources.

Planting trees in patches or "islands" simulates the nucleation model of succession (sensu Yarranton and Morrison 1974) and may be a less expensive restoration approach than establishing plantations. Nucleation occurs when early-successional vegetation establishes in patches that spread outward clonally and/or by facilitating the seed dispersal and establishment of later-successional species (Yarranton and Morrison 1974). Previous research on abandoned tropical agricultural lands suggests that this model may apply. For example, numerous studies have demonstrated that remnant trees (e.g., Guevara et al. 1992, Duncan and Chapman 1999, Otero-Arnaiz et al. 1999, Galindo-Gonzalez et al. 2000, Slocum 2001, Hooper et al. 2005, Schlawin and Zahawi 2008), patches of early-colonizing shrubs (Vieira et al. 1994, Holl 2002, Puyravaud et al. 2003), and rotting logs (Peterson and Haines 2000, Slocum 2000) enhance seed rain and seedling establishment in their immediate vicinities.

The nucleation model shows a great deal of promise as a restoration tool because it simulates a pattern of natural recovery. However, only a few studies have tested its application to restoration (Robinson and Handel 2000, Zahawi and Augspurger 2006, Benayas et al. 2008). The only previous study testing the role of planted tree islands in facilitating recovery of tropical forest demonstrated that bird activity, seed rain, and seedling establishment were elevated in tree islands compared to open pasture within the first two years after planting (Zahawi and Augspurger 2006).

The potential for island expansion, a critical component of the nucleation model (Auld and Coote 1980), is not well understood. The majority of previous studies which suggest support for the nucleation model have demonstrated only higher establishment and survival of seedlings below shrubs or trees compared to open areas (Debussche and Isenmann 1994, Verdú and García-Fayos 1996, Carriere et al. 2002, Franks 2003, Garcia and Obeso 2003, Russell-Smith et al. 2004; but see Schlawin and Zahawi 2008), rather than recording

whether there is enhanced seed deposition beyond the edge of the nuclei in the potential expansion zone as reported by Zahawi and Augspurger (2006). Last, no evaluations have compared the restoration potential of small tree nuclei to larger plantations.

Another issue to consider in applying the nucleation model to restoration is the importance of island size. A few studies have found higher seed rain and tree seedling density and diversity in larger rather than smaller patches (Campbell et al. 1990, Cook et al. 2005, Zahawi and Augspurger 2006), whereas others have found no effect (Guevara et al. 1986, Robinson and Handel 2000, Holl 2002). Larger islands are likely to be more attractive to dispersers because they are more highly visible and provide greater amounts of habitat for cover and foraging. Prior research suggests that birds are more likely to visit larger islands and stay there longer, potentially resulting in more seed dispersal and seedling establishment (Zahawi and Augspurger 2006, Fink et al. 2009). Nonetheless, concrete information is lacking on what constitutes a "sufficiently large" island and whether there is a minimum critical size threshold for tree islands to function as effective regeneration nuclei.

The location of a restoration site within the landscape often plays a critical role in determining seed rain dynamics. Past studies in second growth habitats in the tropics have demonstrated the importance of remnant forest proximity for dispersal and establishment of zoochorous plants (Thomlinson et al. 1996, Harvey 2000a, b, Zanne and Chapman 2001, Chinea 2002, Ferguson et al. 2003), whereas others have shown no such trend (e.g., Guevara et al. 1986, Aide et al. 1996, Zahawi and Augspurger 2006, Dosch et al. 2007, Pejchar et al. 2008). If landscape-scale factors, such as the amount of forest cover in the surrounding landscape, are important drivers of seed dispersal patterns, seed density and diversity should be greater in areas with more forest cover nearby. Conversely, if seed dispersers preferentially utilize restored areas planted with trees, then local-level factors such as planting design may more strongly influence the nature of seed dispersal. Understanding the importance of the extent of surrounding forest on recovery is critical to prioritizing areas and methods of restoration in fragmented landscapes.

Key groups of seed dispersers may respond differently to restoration approaches and the amount of surrounding forest cover. In areas that have been altered extensively by human activity, larger vertebrates are often rare or absent, and small-bodied animals, such as birds and bats, are the primary seed dispersers (e.g., Estrada et al. 1993, Nepstad et al. 1996, Galindo-Gonzalez et al. 2000, Barrantes and Pereira 2002, Martinez-Garza and Gonzalez-Montagut 2002, Guevara et al. 2004, Griscom et al. 2007). Previous studies indicate that many forest birds avoid open areas (DaSilva et al. 1996) and use woody vegetation for foraging and movement through agricultural areas (Perfecto et al. 1996, Estrada et al.

2000), whereas bats are more likely to frequent open habitat (Deforesta et al. 1984, Medina et al. 2007). However, the relative roles of each of these important disperser groups have rarely been compared, particularly in restoration settings.

The objective of this study was to test the potential of applied nucleation as a restoration strategy in a region characteristic of Central American agricultural landscapes. We measured seed rain for 1.5 years beginning two years after applying three 50 × 50 m restoration treatments: control (natural regeneration), islands (planting native tree nuclei of three sizes: 4 × 4 m, 8 × 8 m, 12 × 12 m) and plantation (planting uniformly with tree seedlings). In order to evaluate patterns of seed rain across a range of conditions and make results generalizable on a meaningful spatial scale, we replicated the study at 11 sites across a 100-km^2 area of southern Costa Rica. Sites were distributed across a gradient of remnant primary forest cover in the surrounding landscape, enabling us to measure the effect of proximity to seed sources on seed rain. The specific goals of this research were to (1) compare the effect of experimental treatments on the density and species composition of seed rain; (2) determine the effect of island size on the density and species composition of seed rain; (3) measure the potential for island expansion by quantifying seed rain at several distances from island edges; (4) compare the relative seed dispersal contributions of bats and birds; and (5) evaluate whether local restoration strategy or amount of surrounding remnant forest more strongly affected patterns of seed deposition.

METHODS

Study area.—The study was conducted from February 2006 through August 2008 at 11 ~1-ha experimental sites distributed across a ~100-km^2 area between the Las Cruces Biological Station (LCBS; 8°47′7″ N, 82°57′32″ W) and the town of Agua Buena (8°44′42″ N, 82°56′53″ W) in southern Costa Rica (Appendix C). The forest in this region is classified as a tropical montane rain forest by Holdridge et al. (1971). Sites range in elevation from 1100 to 1300 m above sea level and mean annual rainfall is ~3500 mm with a distinct dry season from December to March. The region was largely forested until approximately 60 years ago when government-sponsored immigration led to the development of land for small-scale agriculture. Between 1950 and 1980, forest was cleared extensively for coffee production; however, with the collapse of the coffee market beginning in the early 1990s, much of the land under agriculture was converted to cattle pasture (Rickert 2005). As is typical of much of Central America, the landscape is a highly fragmented mosaic of small remnant forests, patches of active agriculture, fallow plots, and pasture. Estimates show that less than 27% of the land in a 15-km radius surrounding LCBS remains forested (Daily et al. 2001).

Experimental design.—Seven experimental sites were established in 2004 and four in 2005 (hence 2.5 and 1.5 years of tree growth prior to initiating this study in 2006); site establishment was spread over two years due to the logistics of setting up a large-scale project. Because of high variability in the rates of tree growth, substantial overlap in mean tree height existed between the two planting years at the start of seed rain measurements (105.0–457.4 cm for 2004 sites and 124.0–221.9 cm for 2005 sites; K. D. Holl and R. A. Zahawi, *unpublished data*). The sites are separated by a minimum of 500 m and are representative of lands being removed from agriculture in the region. All of the sites had been farmed for ≥18 years, usually first for coffee and then pasture, and most are steeply sloping (see Appendix B for details). Forest cover within 100 and 500 m radii from the center of each experimental plot was hand digitized from ortho-rectified 2005 aerial photographs and comprehensively ground checked. Forest cover spans a range from <1% to 66% within a 100-m radius surrounding the plots and from 9% to 89% in a 500-m radius (Appendix C).

At each site, we established three 0.25-ha (50 × 50 m) plots separated by >5 m. Each plot received one of three treatments: control, island, or plantation (Fig. 1; see Plate 1). No trees were planted in the control treatment to allow for natural regeneration. The plantation treatment was uniformly planted with tree seedlings. The island treatment was planted with six islands of tree seedlings (hereafter referred to interchangeably as nuclei or islands) of three sizes: two each of 4 × 4 m, 8 × 8 m, and 12 × 12 m. Nuclei were separated by a minimum of 8 m (Fig. 1). The same planting density of seedlings was used in both treatments; however, 313 individuals were planted in plantations and 86 in islands. Two of the island plots differed slightly from the standard layout due to space constraints on the available land: the rows of nuclei were offset at one site and were separated by more than the normal distance at another site. Preliminary analyses with and without data from these two sites showed similar results; therefore, data were included in the results presented.

Following clearing of all aboveground vegetation in each plot, we planted seedlings of four tree species that have high regional survival, rapid growth, and extensive canopy development within a couple years (Nichols et al. 2001, Jiménez et al. 2002, Carpenter et al. 2004, Calvo-Alvarado et al. 2007). Two native hardwood species, *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), produce valuable timber and have high native woody species establishment in their understory (Cusack and Montagnini 2004). Two naturalized softwood species, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae), are fast-growing N-fixing species widely used in agricultural intercropping systems to provide shade and increase soil nutrients, and have extensive branching architecture and fruit (*Inga*) that attract birds
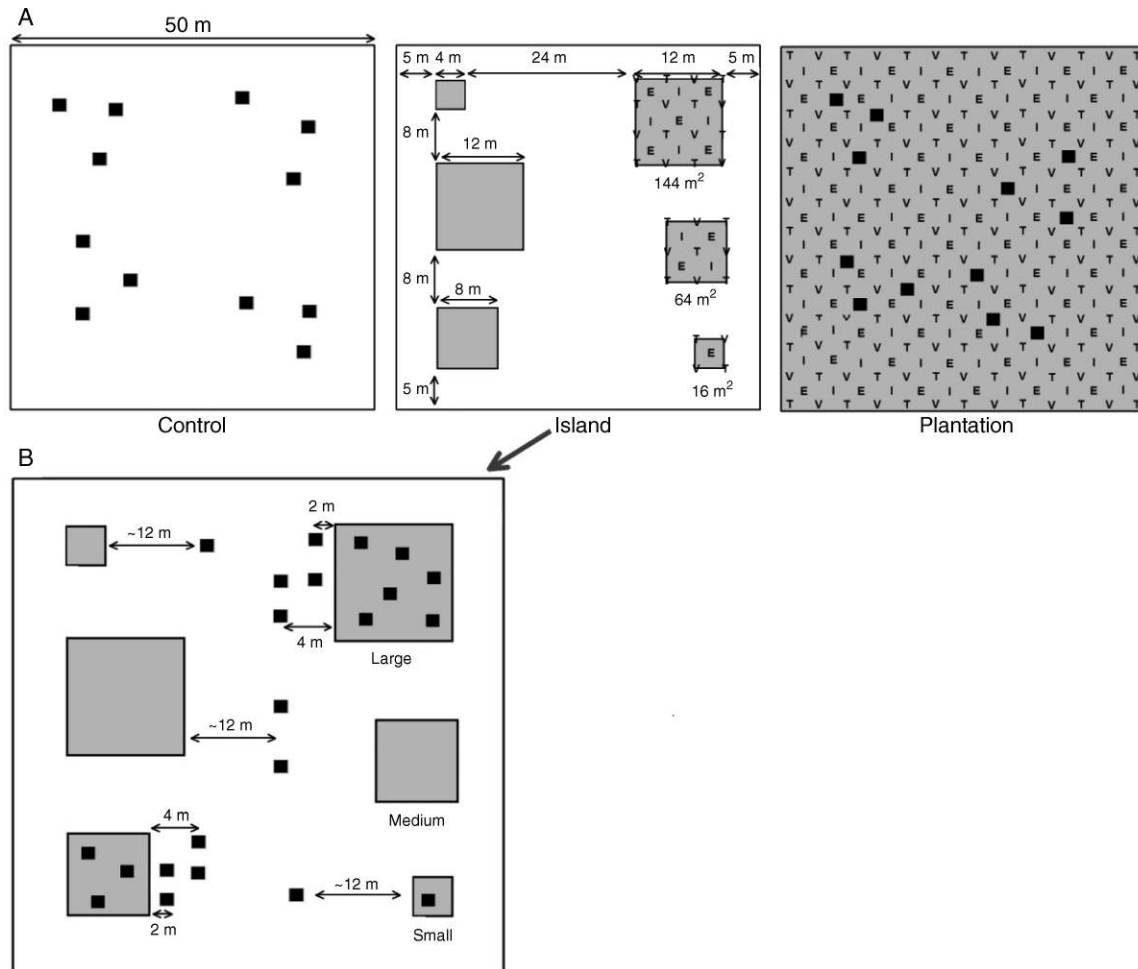
Fig. 1. (A) Experimental design, illustrating one possible layout of a site with three 50 × 50 m plots. Treatment and island locations were randomized with the constraint in the latter that there was always one island of each size (4 × 4 m, 8 × 8 m, 12 × 12 m) on the left and right sides of the plot. Gray indicates areas that were planted with trees separated by 2.8 m along the diagonal and 4 m in rows. (T = *Terminalia amazonia*, V = *Vochysia guatemalensis*, E = *Erythrina poeppigiana*, I = *Inga edulis*). Black squares show the locations of seed traps. (B) Placement of seed traps (black squares) in an island plot. Groups of four traps were placed at 2 m and 4 m from the edges of medium and large islands and along midpoints between islands (~8–12 m from island edges).

(Pennington and Fernandes 1998, Nichols et al. 2001, Jones et al. 2004). In both island and plantation plots, seedlings were planted in alternating rows of hardwoods (*Terminalia* and *Vochysia*) and softwoods (*Erythrina* and *Inga*; Fig. 1). Species were planted alternately 4 m apart, and rows were separated by 2 m and offset by 2 m so that all seedlings were separated by a minimum of 2.8 m which is standard for reforestation in the region (Calvo-Alvarado et al. 2007).

All of the plots (including the control) were cleared to ground level by machete at ~3-month intervals for the first 2.5 years to allow planted tree seedlings to grow above existing grasses and forbs. Vegetation at the termination of clearing was dominated by a mix of native and nonnative grasses, including *Axonopus scoparius*, *Paspalum* spp., *Pennisetum purpureum*, and *Urochloa brizantha*, and ruderal herbs, such as

Heterocondylus vitalbae, *Pteridium arachnoides*, and *Spermacoce assurgens* (K. D. Holl and R. A. Zahawi, *unpublished data*).

Seed trap design.—Seed traps were constructed from fine-gauge (0.5 × 0.5 mm) mosquito netting suspended in an inverted pyramid from circular wire hoops and mounted on 50 cm tall legs (trap collecting area = 0.25 m²). One or two large rocks were placed in the bottom of each trap to prevent the mesh being turned inside out by wind. Seeds dispersed by ground-dwelling mammals were excluded from collection; previous research on seed dispersal by mammals in the study plots showed these events to be extremely rare (Cole 2009a).

Data collection.—We collected seeds twice monthly in 12 traps in each control and plantation plot and in 22 traps in island plots (Fig. 1). More traps were placed in island plots to enable comparisons of patterns of seed

rain within the plot, including island size and expansion. To compare seed rain in islands of different sizes, one, three, and six traps were randomly placed within one small, medium, and large island, respectively (sampling intensity ~1%). Selection of the island that received traps was random; however, if a selected island had poor planted tree survival (<50%) the better-developed of the two islands was selected. This was done because a primary objective of the study was to assess the effect of nuclei size and poor tree survival substantially reduces island area. To quantify seed rain in the unplanted area adjacent to each tree island (expansion zone), two traps each were placed at both 2 and 4 m away from the base of the outer trees of medium and large islands. Lastly, four traps were placed along the center of the plot between rows of islands (~12 m from island edges; Fig. 1). Seed rain near the edge of small islands was not quantified. Traps in the control and plantation were placed in groups of three at the edges of four 8 × 8 m permanent sampling plots, each in a different quadrant of the plot (Fig. 1). This placement enabled seed traps to be paired with other research monitoring changes in vegetation structure and species composition. Fig. 2 shows the differences between island interior and the expansion zone outside of the planted areas.

To assess the relative contributions to the seed rain by birds and bats, we placed 12 daytime and 12 nighttime traps in control and plantation treatments at a subset of sites. Traps were either opened or closed at ~05:00–06:00 and ~17:00–18:00 each day. Given the time necessary to open and close traps twice daily within a narrow time window and the travel distance among sites, we compared bat and bird dispersal for six weeks from June to July 2007 (peak of the fruiting season) and at four sites only. We surveyed two sites at a time in alternating weeks, so we collected data at each site for three weeks. Trap contents were collected once weekly.

To examine how differences in tree height affected seed dispersal, we measured the height of all planted trees in island plots and approximately one-third of trees (randomly selected) in the plantations (K. D. Holl and R. A. Zahawi, *unpublished data*). Percent overhead cover was measured near each seed trap in the middle of the study (June–July 2007) using a spherical densiometer (mean percent cover ± SE in each site: control = 6.1 ± 1.0; island = 9.5 ± 2.2; plantation = 54.5 ± 10.9). In 2007, we also censused vegetation in four 16 × 16 m plots at each of six remnant forest patches adjacent to high forest cover sites in order to establish a reference baseline for mid–late successional species that could serve as sources of seeds (R. A. Zahawi and K. D. Holl, *unpublished data*).

Seed collection and identification.—The contents of all traps were collected twice monthly from February 2006 to September 2008 (18 months); day- and nighttime traps were collected weekly as described above. Traps that were damaged by wind, livestock, or humans were excluded from the data for that collection period. Heavy

FIG. 2. (Top) A medium island with seed traps placed in the expansion zone in the grass and (bottom) the interior of a large island.

leaf litter and branches that fell into traps were brushed to remove any seeds adhering to their surface and discarded in the field. Remaining trap contents were placed in manila envelopes and dried at ~65°C for several days. Seeds were then sorted, identified, and counted using hand lenses (10× magnification) and a dissecting microscope for very small seeds. All seeds were quantified except for grasses, because the purpose of this study was to examine factors limiting forest regeneration rather than species dominant in abandoned pastures (i.e., introduced pasture grasses). Fruiting

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TABLE 1. Percentage of total, total number of species, and mean density ($\pm$SE) of seeds by habit, successional stage, and dispersal mode in each experimental treatment.

	Control			Island		
Category	Percentage of total	Number of species	Density (seeds·m^{-2}·yr^{-1})	Percentage of total	Number of species	Density (seeds·m^{-2}·yr^{-1})
Habit						
Herb	59	34	952.7^a ± 547.5	46	33	710.3^a ± 334.1
Shrub (anem.)	5	2	79.4^a ± 35.2	10	2	156.4^a ± 75.4
Shrub (zoo.)	13	19	201.4^a ± 62.7	22	19	345.9^a ± 116.4
Tree (anem.)	13	4	202.1^a ± 102.4	3	6	45.4^a ± 17.9
Tree (zoo.)	5	12	87.1^a ± 13.9	14	16	210.4^{ab} ± 52.7
Liana	<1	5	6.0^a ± 3.6	<1	7	7.6^a ± 3.6
Unknown	4	34	62.6 ± 20.7	5	33	76.7 ± 40.4
Successional stage						
Ruderal herb	67	38	1075.1^a ± 556.0	55	35	851.2^a ± 390.0
Early	26	30	420.3^a ± 6.8	36	34	556.2^a ± 138.2
Mid–late (zoo.)	<1	6	3.7^a ± 2.0	<1	10	11.5^a ± 7.1
Mid–late (anem.)	1	3	10.7^a ± 9.0	<1	5	1.4^a ± 0.7
Dispersal mode						
Animal	24	80	378.9^a ± 77.9	44	90	679.0^a ± 151.4
Wind	71	26	1135.0^a ± 544.6	49	23	761.7^a ± 393.7
Gravity	5	6	87.5^a ± 28.8	7	6	112.0^a ± 44.8
All seeds	40	112	1601.4^a ± 609.1	39	118	1552.7^a ± 465.3

Notes: Values for the control and plantation are for all 12 traps in each treatment combined. Values for the island plot are from 12 traps (four within planted areas, eight in unplanted areas). Anemochorous (anem.) and zoochorous (zoo.) tree, shrub, and mid–late-successional seeds are shown separately. Means with the same superscript letter are not significantly different ($P < 0.05$) using Tukey's hsd.

plants were collected throughout the region on an ongoing basis to establish a reference collection, and seeds were identified to the lowest possible taxonomic level. Further identifications were made at the Las Cruces Biological Station herbarium (LCBS) and by consultation with several botanists. Vouchers of each species were stored in 70% alcohol and were deposited at LCBS.

Data analyses.—To compare differences in seed rain species composition among sites, we characterized seeds by (1) growth form (herbs, shrubs, trees, lianas, and unknowns); (2) successional stage (ruderal herbs, early successional, and mid–late successional); and (3) dispersal mode (animal, wind, gravity/explosive). The category "ruderal herbs" is composed of weedy species common throughout active agricultural lands. Although some of the planted *Erythrina poeppigiana* and *Inga edulis* trees set seed during the course of the study, no seeds of these species were recorded in traps. Therefore, the "tree" categories refer to seeds that were dispersed into plots from outside sources and do not reflect input from planted species.

To equalize the number of traps across treatments for plot-level analyses, 12 traps (out of 22) from each island plot were selected in proportion to planted and unplanted areas in the treatment for comparison with control and plantation treatments (four traps in tree island interiors, two traps at 2 m, and three traps each at 4 and 12 m from nuclei edge; Fig. 1). All island plot traps were used for analyses of nuclei size and distance from nuclei edge within island plots. In all analyses of

seed density we used averaged data from the 1.5-year study for the categories described in the previous paragraph. Units are either seeds·m^{-2}·yr^{-1} or seeds·m^{-2}·d^{-1} (bird and bat data only). We also compared the total number of species (species density) recorded in each plot for each category.

Our experiment was set up as a randomized complete block design with site as the blocking factor. Preliminary analyses indicated no significant differences in seed densities between sites planted in 2004 and 2005 ($P > 0.05$ in all cases), so sites from both years were combined for all analyses. We initially examined the effects of local restoration treatment (control, island, and plantation) and landscape-level characteristics (percent forest cover in the surrounding landscape) for all seed categories using the following general linear model:

$$y = \text{Treatment} + \text{Block} + \%\text{Forest Cover} + \text{Treatment} \times \%\text{Forest Cover} + \text{error}.$$

Percent forest cover includes both primary and secondary forests ($\geq$10 years growth), since preliminary analyses showed no differences in trends when they were analyzed separately. Separate analyses were performed using measures of surrounding forest cover at 100 and 500 m radii from the center of each plot, as we had insufficient replication to include both distances and their interactions with treatments in the model simultaneously. As forest cover at both distances did not significantly affect overall seed or species densities in any of the broad categories outlined at the beginning of this section ($P > 0.10$), they were removed from the model. We used the same model

TABLE 1. Extended.

Plantation		
Percentage of total	Number of species	Density (seeds·m^{-2}·yr^{-1})
25	32	208.8[a] ± 33.4
2	2	20.4[a] ± 9.3
24	20	197.8[a] ± 41.2
9	6	71.5[a] ± 31.6
32	15	266.1[b] ± 64.5
<1	5	3.7[a] ± 1.0
6	26	50.3 ± 18.2
30	37	243.3[a] ± 37.1
51	27	417.3[a] ± 54.5
<1	10	1.9[a] ± 0.7
<1	5	1.7[a] ± 0.8
67	79	551.3[a] ± 96.3
31	21	252.6[a] ± 46.5
2	5	15.8[a] ± 4.8
21	106	551.3[a] ± 96.3

to test for local and landscape-level effects on the seed densities of the seven most common zoochorous and anemochorous tree species (mean >10 seeds·m^{-2}·yr^{-1}; Table 2). Because tree growth varied greatly among sites, we tested whether tree cover influenced the arrival of zoochorous tree seeds by regressing seed densities in each island and plantation treatment against tree height and overhead cover. We did not do this analysis for controls because there were no trees planted in these plots, and there were very few naturally established trees >2 m tall during the period of this study.

The effects of nuclei size and distance from nuclei edge on seed rain densities within the island treatment were compared using a randomized block one-way analysis of variance (ANOVA) with location within island plot (small, medium, or large island; 2 m, 4 m, or 12 m from edge) as the explanatory variable. We focused this analysis on zoochorous trees and shrubs as they are of key importance to nuclei expansion and patterns of anemochorous seed rain should not be affected by plantings. Finally, we compared the relative contributions to the seed rain of birds and bats using a randomized-block two-way ANOVA with treatment (control or plantation), time of day (day or night), and their interactions.

In all analyses, seed density data were square-root transformed and the residuals examined to determine that the data met assumptions of normality and homogeneity of variances (Zar 1996). Species density and percent forest cover data were normally distributed and required no transformations. We used Tukey hsd post hoc tests to determine significant differences among treatments when appropriate. Throughout, means ± 1 SE are reported and $P < 0.05$ is considered significant.

All analyses were conducted using Systat 12.0 (Systat Software 2007).

RESULTS

Seed rain characteristics.—A total of 251 768 seeds were collected in control, island, and plantation treatments over the 1.5-year sampling period. Seeds represented 168 species from at least 43 families. Nearly half (45.7%) were Asteraceae, most of which are anemochorous. The next most common families were Solanaceae (10.6%), Melastomataceae (7.9%), and Urticaceae (7.2%), all of which are zoochorous. Of all seeds collected, 77 species (comprising <6 % of the total number of seeds) could not be identified; it was possible, however, to determine dispersal mode in most cases. Herbs, mainly common ruderal species, accounted for 44% of all seeds and 31% of all species. Forty-eight percent of all seeds and 75% of all species were zoochorous, whereas 44% of seeds and 20% of all species were anemochorous. Fourteen percent of seeds were zoochorous trees (22 species) and 5% were anemochorous (6 species). A small fraction of the seeds that arrived in the plots (0.4%) were classified as mid-late successional species (Table 1). Appendix A provides a summary of all species of seeds grouped by growth form, successional stage, and dispersal mode.

The most commonly dispersed zoochorous and anemochorous trees were small-seeded (maximum diameter < 2.0 mm) early-successional species commonly found in edge habitat, along roadsides, and fallow fields. Of the 146 tree species surveyed in forests adjacent to six of the experimental sites (R. A. Zahawi and K. D. Holl, *unpublished data*), only 11 species were recorded in the seed traps. Five early-successional zoochorous tree species accounted for 99.3% of all animal-dispersed tree seeds collected (Table 2). Similarly, a single anemochorous tree species, *Heliocarpus appendiculatus,* accounted for 89.1% of wind-dispersed tree seeds (Table 2).

As with previous studies, we noted distinct seasonal patterns in the seed rain. The vast majority of anemochorous tree seeds (88.5%) fell during the dry season between December and March and 78.4% of zoochorous tree species were deposited during the early part of the wet season from April to July (Fig. 3). The total number of seeds dispersed during the dry season and the first half of the wet season in the two years was similar.

Treatment and landscape effects.—The amount of forest cover within 100 and 500 m radii of the experimental plots did not significantly affect either the seed rain or species density of any category ($F \leq 3.2$, df = 2, 17, $P > 0.05$ in all cases) and was therefore removed from the statistical model for these analyses. Plantations received nearly three times as many zoochorous tree seeds (266.1 ± 64.5) as controls (87.1 ± 1 3.9) ($F = 3.8$, df = 2, 20 $P = 0.0405$); island plots received an intermediate number (210.4 ± 52.7) but were not significantly different from either treatment due to high variances among sites (Table 1). Species densities did not

TABLE 2. Mean seed density (±SE) of the seven most commonly dispersed tree species in control, island, and plantation treatments (includes all species with mean density >3 seeds·m^{-2}·yr^{-1}).

| | | | Density (seeds·m^{-2}·yr^{-1}) | | |
Species	Family	Dispersal mode	Pasture	Islands	Plantation
Heliocarpus appendiculatus	Tiliaceae	wind	191.4^a ± 100.1	44.12^a ± 18.0	69.8^a ± 31.8
Cecropia peltata†	Urticaceae	bird, bat	21.3^a ± 8.0	43.8^a ± 9.7	105.2^b ± 46.0
Cecropia obtusifolia	Urticaceae	bird, bat	17.7^a ± 6.3	51.0^b ± 16.1	44.3^b ± 12.4
Conostegia rufescens	Melastomataceae	bird, bat	15.8^a ± 8.9	18.1^{ab} ± 7.8	70.1^b ± 34.7
Miconia trinervia	Melastomataceae	bird, bat	17.0^a ± 9.2	43.3^a ± 19.0	22.3^a ± 7.8
Conostegia xalapensis	Melastomataceae	bird, bat	11.0^a ± 2.8	45.7^a ± 22.7	22.0^a ± 4.4
Ulmus Mexicana	Ulmaceae	wind	9.9^a ± 8.9	0.8^a ± 0.6	0.5^a ± 0.2

Notes: Seed density is ranked by decreasing overall abundance. All of the zoochorous species and one of the anemochorous species (*Heliocarpus appendiculatus*) are common early-successional species. *Ulmus mexicana* is a late-successional species often occurring as a remnant in agricultural lands. All trees are small-seeded (<2.0 mm diameter). Treatments with the same superscript letter are not significantly different ($P < 0.05$) based on Tukey's hsd multiple comparisons.

† Seed density of *Cecropia peltata* in plantations, but not other treatments, increased with increasing forest cover within a 100-m radius.

significantly differ among treatments for any other seed category.

Seed rain density of *Cecropia peltata*, a commonly dispersed zoochorous tree, was higher in plantation plots (but not other treatments) with more forest cover in the surrounding 100 m area (forest cover × treatment interaction; $F = 3.6$; df = 2, 17; $P = 0.0486$). Deposition of this species in plantations was five and two times greater than in control and island treatments, respectively (Table 2). Seed density of the other common zoochorous trees was not related to forest cover ($F \leq 3.4$, df = 2, 17, $P > 0.05$). *Cecropia obtusifolia* was dispersed in greater amounts to the plantation compared to the control plot ($F = 3.8$; df = 2, 20; $P = 0.0397$), and *Conostegia rufenscens* was dispersed in greater densities to both of the planted treatments compared to the controls ($F = 6.4$, df = 2, 20, $P = 0.0071$; Table 2). Seed rain densities of

individual anemochorous tree species did not differ as a function of treatment or percent forest cover.

As is typical for seed rain data, there was high among-site variability in patterns of seed deposition. For example, nearly 4.5 times as many herbaceous seeds were deposited in control plots compared to plantations, but 59.9% of all herbaceous seeds collected in control plots arrived at a single site. Similarly, there was a tendency for more anemochorous tree seeds to arrive in control plots compared to other treatments but this was likely due to very local-level factors. Specifically, the presence of several *Heliocarpus appendiculatus* trees near the control plot of one site accounted for 31.6% of anemochorous tree seeds collected. Surprisingly, neither tree height nor percent overhead cover explained a significant percentage of among site variance in levels of
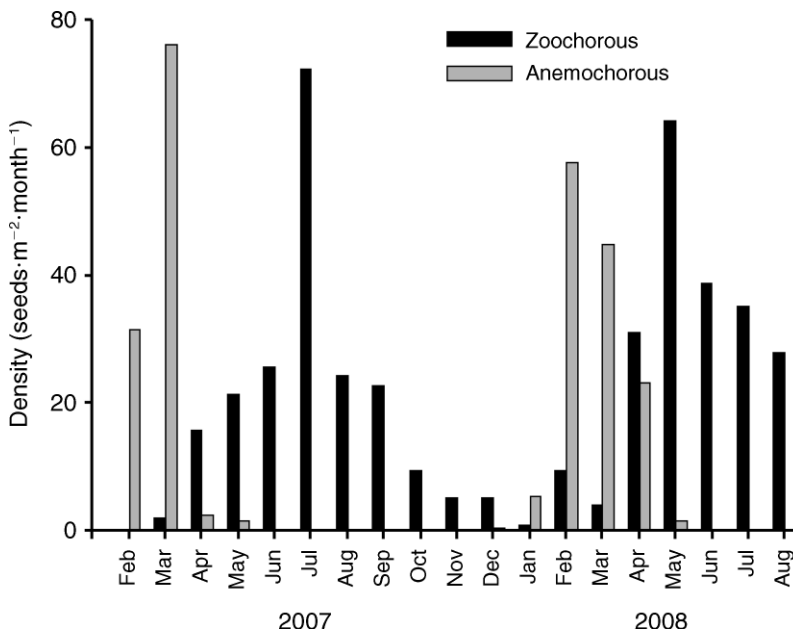

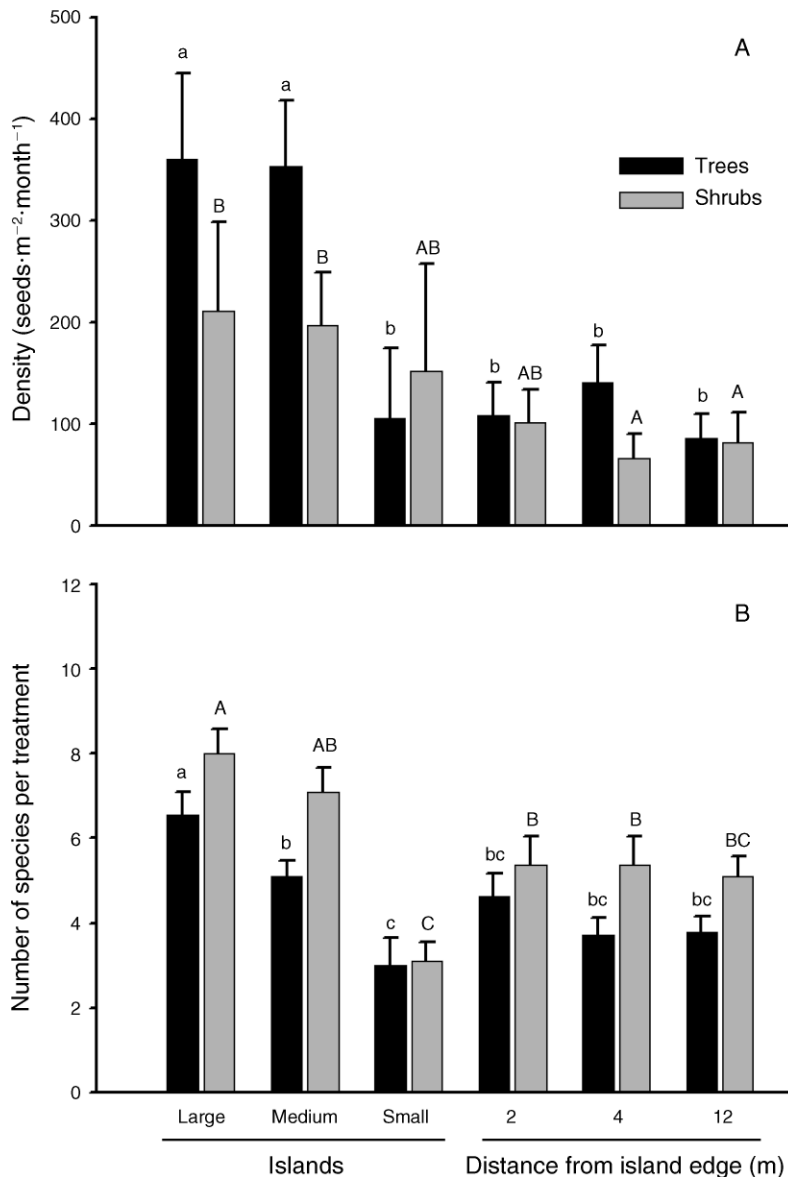FIG. 3. Seasonal patterns of zoochorous and anemochorous tree seeds falling in the experimental sites.

FIG. 4. (A) Zoochorous tree and shrub seed and (B) species densities at each location within island plots. Treatments with the same letter are not significantly different ($P < 0.05$) based on Tukey's hsd multiple comparisons among trees (lowercase letters) and shrubs (uppercase letters). Error bars are +SE.

zoochorous seed density in plantation or island plots ($r^2 < 0.03$; $P > 0.05$ in all cases).

Island size and distance from island edge.—More zoochorous tree seeds were dispersed to large and medium-sized islands than to either small islands, or areas in the expansion zone at 2, 4, or 12 m away from island edges ($F = 11.2$, df = 5, 50 $P < 0.0001$; Fig. 4). There was no significant difference between the zoochorous tree seed density in small islands and traps in the expansion zone or among traps at different distances from island edges. Similarly, more zoochorous tree species arrived in the large island compared to the small island and all the expansion zone locations ($F = 9.0$; df =

5, 50; $P < 0.0001$); medium islands received more species than small islands but were similar to all other locations within the island plots.

Dispersal of zoochorous shrubs showed a similar but less consistent pattern (Fig. 4). Both large and medium islands received more shrub seeds than several of the expansion zone locations ($F = 4.1$; df = 5, 50; $P = 0.0032$) but were similar to the small islands. More zoochorous shrub species fell in large compared to small islands and all other expansion zone locations, whereas medium islands received more shrub species than small islands but were similar to all other locations within the island plots ($F = 11.5$; df = 5, 50; $P < 0.0001$; Fig. 4).
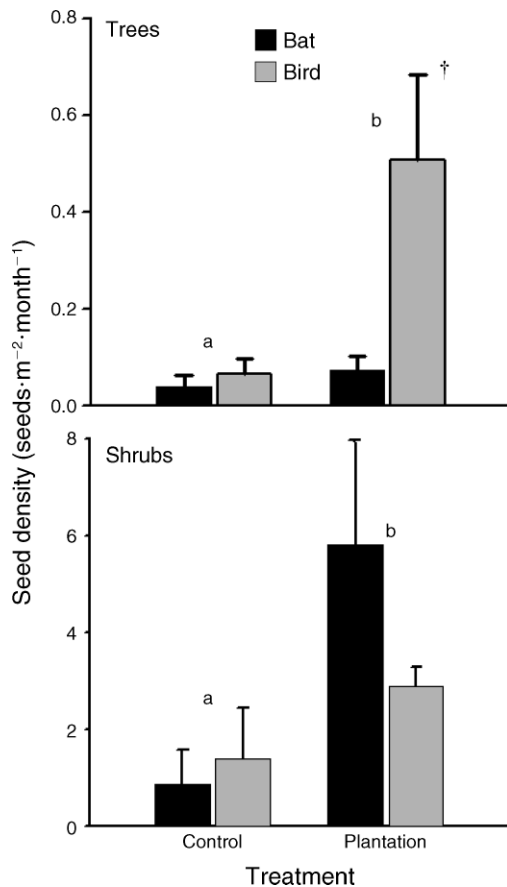
FIG. 5. Mean seed density of tree and shrub seed by disperser and treatment. Treatments with the same letter are not significantly different ($P < 0.05$) based on ANOVA. Error bars show +SE. Birds dispersed significantly more tree seeds than did bats in the plantation treatment (shown by a dagger).

Seed dispersal by birds and bats.—Seed dispersal during the day (birds) and at night (bats) differed significantly as a function of planting treatment (treatment × time of day interaction; $F = 8.2$; df = 1, 9; $P = 0.0186$; Fig. 5). Deposition of tree seeds by bats was similar in controls and plantations, whereas birds dispersed nearly seven times more seeds in plantations than control plots (islands were not assessed in this study). As a result of the greater seed rain from birds, more zoochorous tree seeds were deposited in the plantations than the control plots in the four sites included in this portion of the study ($F = 13.1$; df = 1, 9; $P = 0.0056$). Zoochorous shrub seeds were also dispersed in greater quantities to plantations than controls ($F = 15.7$; df = 1, 9; $P < 0.0033$) but bats and birds contributed in similar quantities to the shrub seed rain (Fig. 5).

DISCUSSION

General overview.—The results of this study lead to several conclusions regarding applied nucleation as a restoration strategy and patterns of forest succession on post-agricultural lands. First, we found that planting trees both in plantations and islands substantially enhanced the arrival of small tree seeds dispersed by birds within the first 2–4 years after planting, but did not affect arrival by wind, gravity, or bats. Second, our results concur with the findings of previous studies showing that the dispersal of primary forest species is strongly limited in fragmented landscapes regardless of the restoration strategy used (Holl 1999, Harvey 2000b, Dosch et al. 2007). Third, we found that the amount of forest cover within the surrounding 100- and 500-m landscape had a relatively minimal effect on seed dispersal compared to tree planting strategy during this early stage in succession. Finally, there appears to be a minimum critical size threshold for tree islands necessary to increase the deposition of zoochorous tree seeds.

Restoration treatments.—Based on past studies, we predicted that dispersal of zoochorous seeds would be higher in plantation and island treatments than in the control plots because the areas planted with trees would be attractive to frugivores and would provide more habitat for foraging and protection (e.g., Parrotta et al. 1997, Lamb et al. 2005, Zahawi and Augspurger 2006, Orozoco Zamora and Montagnini 2007, Fink et al. 2009). Indeed, three times as many zoochorous tree seeds arrived in plantations as in controls. Island plots were more similar to plantations in terms of the number of seeds deposited. The number of seeds arriving in the island plots was probably slightly lower than plantations at this stage in the development of the nuclei because of the relatively high proportion of open (~85%) to planted areas (~15%). In fact, the mean number of tree seeds per trap collected inside the planted areas of the island treatments (295.1 ± 90.9) was similar to the plantations (266.1 ± 64.5), but as the results of the within-plot study of the island treatment suggest, seed deposition beyond the edge of the areas planted with trees dropped sharply.

Our results also suggest that there is a minimum size threshold for islands necessary to be attractive to seed dispersers and to enhance seed rain. Deposition of zoochorous tree seeds was higher in both the large and medium islands compared to the small island or any of the areas in the expansion zone. Although patterns of shrub seed dispersal were not as sharply defined, large and medium islands tended to have greater seed rain compared to areas in the expansion zone. Observations of bird activity at six of our sites also showed higher bird visitation and foraging in the large and medium islands compared to the smaller islands (Fink et al. 2009). Similarly, Zahawi and Augspurger (2006) found higher levels of zoochorous tree seed deposition in larger tree islands (64 m²) planted with *Gliricidia sepium* compared to smaller islands (16 and 4 m²). From a restoration perspective, these findings suggest that nuclei >64 m² are more effective for facilitating forest recovery than smaller nuclei, at least in the seed-dispersal stage.

PLATE 1.   Photo of one experimental site taken in 2006 at the initiation of the study. The plantation (P) is outlined on the left, the control (C) is in the center, and the island treatment (I) is on the right. Photo credit: R. J. Cole.

We did not find increased levels of tree or shrub seed deposition in the expansion zone near the outside of island edges, which is consistent with previous studies reporting a dramatic drop in the density and diversity of zoochorous seed rain only a few meters away from the edge of forest (Holl 1999, Cubina and Aide 2001, Dosch et al. 2007). Zahawi and Augspurger (2006) found similar levels of seed density in the interior of planted tree patches and in a 1-m expansion zone; a smaller area than we measured. Although studies in distinct habitats often show that seed rain is higher under remnant trees and other types of vegetation that provide perching structures (e.g., Guevara et al. 1986, Harvey 2000b), there has been relatively little testing to determine whether seed rain is also enhanced beyond the perimeter of the vegetation. If increased levels of seed rain occur only directly beneath established woody vegetation as this study suggests, then island expansion will occur when seeds falling near the periphery establish and grow outwards. It is also possible that patterns of nuclei expansion will be apparent only over longer periods of time than measured in this study. For example, Schlawin and Zahawi (2008) found that remnant trees had a higher density of tree saplings beneath and adjacent to their canopies than farther away >20 years after site abandonment.

Seed dispersal by birds and bats.—The difference in amount of zoochorous tree seeds entering the plantations vs. control plots appears largely to have been due to enhanced bird activity. Birds dispersed >80% more tree seeds in plantations than did bats, whereas contributions to tree seed rain in control plots by both groups of dispersers was similar. Interestingly, the planting treatment appears to enhance dispersal of shrub seeds by both birds and bats: shrub seed density was twice as high in plantations as in controls over the six weeks of this portion of the study. The importance of these major disperser groups appears to vary among neotropical agricultural landscapes. Some studies show that bats disperse more (Medellin and Gaona 1999), similar (Galindo-Gonzalez et al. 2000), or fewer numbers (Harvey 2000b, Gonzales et al. 2009) of species and seeds. It is possible that bats are more effective dispersers of shrub than tree seeds in this region (e.g., Muscarella and Fleming 2007). For example, bats have been shown to be key dispersers of fast-growing early- and mid-successional shrubs in Costa Rican lowland forest (Kelm and von Helversen 2007), dry forests in Panama (Griscom et al. 2007), and wet forest in Mexico (Medellin and Gaona 1999). Further research on the roles of each disperser group in this region would be informative for development of restoration approaches that facilitate seed dispersal by frugivores.

Landscape-level effects.—A major objective of this research was to explore the relative roles of local vs. landscape-level processes driving patterns of seed dispersal. The local factors of tree planting design appeared to have a much stronger influence on the dispersal of zoochorous tree and mid-late successional seeds than the amount of forest within a 100- or 500-m radius. This result is not surprising given that tree seed rain was dominated by only five early-successional

species (99.5% of total zoochorous tree seeds), none of which are restricted to forest habitats. Studies examining seed dispersal and seedling recruitment at distances from forest greater than 10–25 m have often found no consistent trends (e.g., Guevara et al. 1986, Slocum and Horvitz 2000, Slocum 2001, Zahawi and Augspurger 2006). Likewise, research in the region near LCBS has shown no correlations between abundance or diversity of seed rain and forest fragment size (Dosch et al. 2007), total forest area within 10- to 1000-m buffer areas, or with distance to the nearest forest fragment (Pejchar et al. 2008). The structure of vegetation outside of forests can be important to patterns of bird movement, and tropical forest birds have often been shown to frequent the agricultural matrix (e.g., Daily et al. 2001, Sodhi et al. 2005, Peh et al. 2006, Sekercioglu et al. 2007). Nearly half of the bird species in our region have been found in agricultural areas (Hughes et al. 2002), suggesting that the frugivorous species that utilize this landscape are dispersing seeds similarly to both low and high forest cover areas.

An apparent exception to this trend was *Cecropia peltata* which was positively correlated with increasing forest cover surrounding the plantations but not the other treatments. However, it is quite likely that local reproductive trees influenced these patterns. For example, adult *Cecropia peltata* trees were observed growing along forest edges and in fallow fields near three plantation plots where very high levels of seed rain (135 to 522 seeds·m^{-2}·yr^{-1}) were recorded. Similarly, several *Heliocarpus appendiculatus* trees adjacent to a control plot were in all likelihood the sources of 32.8% of all seeds collected for this species, and a large remnant tree near one of the control plots accounted for 79.9% of all *Ulmus mexicana* seeds. These observations point to the importance of local seed sources, as suggested by other studies showing that most seeds are dispersed short distances (Duncan and Chapman 1999, Holl 1999, Mesquita et al. 2001, Ingle 2003, Dosch et al. 2007, del Castillo and Rios 2008).

We found that the vast majority of animal-dispersed seeds arriving at our sites were small-seeded, early-successional species (98.2%). There was little overlap between seed rain and the species surveyed in the forest fragments, even though some of these forests were immediately adjacent to some of our plots. These results support the findings of previous studies in distinct tropical ecosystems showing that many primary forest species and large-seeded species are often absent from the seed rain in human-altered tropical lands (e.g., Holl 1999, Ingle 2003, Martinez-Garza and Howe 2003, Dosch et al. 2007, del Castillo and Rios 2008). It may be necessary to introduce dispersal-limited species through direct seeding or enrichment planting as a secondary phase in the restoration effort (Cole 2009b). It is possible however, that seed rain composition will change in later stages of forest development in the treatments. For example, del Castillo and Perez-Rios

(2008) observed that the species richness and abundance of late-successional seeds increased with the age of successional stands in Mexican montane forests, due, in part, to seed production by local plants. As successional species establish and grow, the plots will become more structurally complex and diverse, potentially attracting a broader range of vertebrate dispersers. The extent of active outplanting vs. allowing succession to proceed over time will ultimately depend on the objectives of the restoration effort.

Implications for tropical forest restoration.—Our results have potentially broad application for restoring forest in fragmented landscapes in the neotropics. They show that "applied nucleation" is a promising restoration strategy when sufficiently large nuclei are planted. In our study, the number of seeds dispersed in island plots was only slightly lower than in plantations, yet the cost of planting was a third of that for plantations. Additionally, we cleared throughout island plots during the 2.5-year maintenance phase of treatment setup but in the actual application of the restoration strategy a land manager could use other maintenance approaches such as clearing only in the islands, immediately around seedlings, or along rows of trees which would further reduce costs and likely increase the rate of island expansion. Moreover, our results suggest that planting tree seedlings in both plantations and larger islands, has broad applicability throughout the landscape given the lesser importance of proximity to remaining forest patches—at least during the early stages of succession and forest recovery.

Ongoing monitoring of naturally establishing seedlings in each of the treatments will be important to determine whether the different levels of zoochorous tree seed inputs actually result in enhanced recruitment of woody vegetation. Nuclei expansion in the island plots, a critical component of the nucleation model of succession, and the effects of each planting treatment on subsequent successional trajectories, bear further observation and should provide key insights into patterns of forest recovery over time. Attention should also be given to more intensive restoration approaches, such as enrichment planting or direct seeding of larger-seeded and later-successional species that fail to recruit because of strong limitations on seed dispersal beyond forest edges.

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APPENDIX A

Seed species collected in seed traps (*Ecological Archives* A020-044-A1).

APPENDIX B

Land use history and characteristics of research sites (*Ecological Archives* A020-044-A2).

APPENDIX C

A photo showing study sites in Coto Brus County in southern Costa Rica (*Ecological Archives* A020-044-A3).