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Edge effects in recruitment of trees, and relationship to seed dispersal patterns, in cleared strips in the Peruvian Amazon

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Abstract We investigated the spatial pattern of tree recruitment 15 years after clear-cutting in two logged strips in the Peruvian Amazon, focusing on differences between seed dispersal modes and cohorts, and relating these to spatial patterns of seed dispersal in the years immediately following clearing. Most trees that recruited in logged strips belonged to taxa dispersed by birds or nonvolant mammals, with smaller numbers dispersed by bats or wind. Seed dispersal patterns differed, with few mammal-dispersed seeds reaching strips, bird-dispersed seeds more abundant near the forest edge than strip centers, and bat- and wind-dispersed seeds more evenly distributed. However, this pattern was not reflected in the tree recruits, except in the deferment cut half of strip 2. Different dispersal modes were differentially represented in different cohorts; for example, in strip 1 birddispersed trees predominated in early cohorts, while trees dispersed by nonvolant mammals predominated in later cohorts. Our finding that trees dispersed by mam-

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mals (which disperse the majority of commercial trees in Amazonia) successfully regenerate from seed in the interior of logged strips highlights the value of maintaining these animals in forest management systems.

Keywords Logged forest · Seedling · Spatial processes · Tropical rain forest

Introduction

Natural forest management, i.e., systems that depend on natural regeneration of trees following logging, is a potentially sustainable land use in tropical rain forest that has less negative impacts on biodiversity than alternative land uses (Dickinson et al. 1996). Understanding postlogging forest regeneration, including the role of seed dispersal, enhances our ability to predict the impacts of management on forest structure and composition, and has the potential to suggest the best management practices that can be implemented to increase yields or maintain biodiversity (Camara-Cabrales and Kelty 2009).

One natural forest management system is the strip clear-cutting, or "Palcazu" system, in which long, narrow (30–40 m) strips are clearcut and all timber is extracted; animal, rather than mechanical, traction is used to minimize soil compaction (Buschbacher 1990; Cornejo and Gorchov 1993; Hartshorn 1989, 1990; Linares Bensimón 1991; Ocaña-Vidal 1992). A small percentage of the surface area is cut each year for the first 30–40 years, after which timber would be extracted from the regenerated forest in the oldest strips.

The composition of forests regenerating after strip clear-cutting in the Peruvian Amazon has been described (Dolanc et al. 2003; Hartshorn and Pariona 1993; Rondon et al. 2009), but the spatial patterns of the recruitment have not been described, nor have they been analyzed in the context of spatial patterns in seed dispersal. Spatial patterns of particular interest are those related to distance from the edge of the uncut, adjacent forest. Tree species with different seed-dispersal modes would be expected to have different potentials to colonize the interior of logged strips; for example, winddispersed seeds are typically better represented in treefall gaps than are animal-dispersed seeds, compared to their representation in forest understory (Loiselle et al. 1996; Martini and dos Santos 2007; Augspurger and Franson 1988). Logged strips are not equivalent to treefall gaps, but share similarities, e.g., removal of the tree canopy, which formed the basis of Hartshorn's (1989, 1990) argument that valuable light tropical hardwoods, which naturally regenerate in gaps, would regenerate well in strips. If differences in seed dispersal with distance from edge impact tree establishment, then distance from the forest edge could structure the spatial pattern of the regenerating stand.

Objectives

In this paper, we report patterns of seed dispersal and tree recruitment of taxa dispersed by different vectors in two cleared strips in the Peruvian Amazon, focusing on patterns from the unlogged forest to the center of the logged strips. Seed deposition in these strips over the first year after felling was described in Gorchov et al. (1993). In this paper, we report patterns of seed dispersal with distance from the forest edge from subsequent years. report distance and temporal patterns of tree recruitment from seed, and evaluate the extent to which recruitment reflects dispersal patterns. In addition to testing whether the strong differences in distance-from-edge patterns of seed deposition by different vectors, which also occurred in tree recruitment, we tested whether temporal patterns were consistent with those proposed for gaps by Schupp et al. (1989). Specifically, was early recruitment dominated by wind-dispersed trees, with lower contribution of small-seeded animal-dispersed (bat- and bird-dispersed) trees and almost no large-seeded animal-dispersed (nonvolant mammal-dispersed) trees? Did recruitment of wind- and small-seeded animal-dispersed seeds decline over time as regeneration occurred?

Methods

Study site

Our study was conducted at the Centro de Investigaciones Jenaro Herrera (CIJH) (4°55'S, 73°40'W), near the Ucayali River approximately 140 km south of Iquitos (Fig. 1). Annual precipitation averages 2,521 mm with June–September generally drier than other months (Ascorra et al. 1993; Rondon 2008; Spichiger et al. 1989). Mean annual temperature is 26 °C (Marengo 1983, cited in Lopez Parodi and Freitas 1990).

Strips were located in low-terrace broadleaf tropical rain forest (Lopez Parodi and Freitas 1990) at about 130-m elevation. A few large trees had been removed from this forest approximately 15–20 years earlier, but its canopy was intact, with a height of 25–30 m. Soils were sandy clay loam with a pH of 3.6–4.0 (unpublished data).

Logging of strips

We cut two strips on level topography, each 30×150 m with the long axis north-south. Strip 1 was cleared at the end of the rainy season (April-May 1989) and strip 2 just after the end of the dry season (October-November 1989). In each strip, lianas were cut several months before clearing to allow connections between trees to weaken, and understory palms and shrubs were cleared. Almost all trees >5 cm dbh were felled, but trees near the edge that were leaning out of a strip were left standing. A "deferment cut" was done in the south half of strip 2, where we left 56 medium-sized (5–28 cm dbh) trees standing. Directional felling was used to ensure that all crowns landed within the 30-m strip.

In strip 1, we avoided cutting trees smaller than 5 cm dbh wherever possible; in strip 2, however, many of these saplings were cut during the understory clearing operation.

Seed rain studies

Seed traps

The seed rain was sampled in each strip during the 2 years following clearing. To quantify seed deposition at several distances from the forest edge, we placed a column of seed traps at three distances, 2.5, 7.5, and 12.5 m, from the forest edge on the west and east sides of strip 1; hereafter referred to as "edge (E)," "intermediate (I)," and "center (C)" locations (Fig. 2).

In each of these six columns we placed 16 traps, for a total of 96 traps. Within each column traps were spaced 7.5 m apart. To compare deposition in the strip to that within the forest, we placed columns of 16 traps in the forest 25 m east and 25 m west of the strip (Fig. 2); hereafter the "forest (F)" location. We assumed that 25 m from the strip was sufficient to eliminate edge effects on seed deposition, as environmental and structural effects are largely confined to within 15 m of rain forest edge (Williams-Linera 1990). Traps were placed on June 15, 1989, shortly after clearing was completed.

Each seed trap consisted of a concave fiberglass screen stapled to a 50×50 -cm frame of PVC tubing mounted on PVC legs so that the rim was 40 cm above the ground. The traps were lined with nylon cloths, which were replaced at semi-monthly intervals for 2 years. The contents of each cloth were carefully checked for seeds and fruits, which were identified with the aid of a reference collection that we developed by collecting and identifying fruiting plant specimens



Fig. 1 Location of the study site, Jenaro Herrera, in northeastern Peru

throughout the study area. Vouchers are deposited at Universidad Nacional Agraria, La Molina in Lima.

To test the effect of deferment cutting (which retained some tree cover) versus clear-cutting on seed deposition, we placed 14 seed traps in each half of strip 2. In each half, seven traps were placed at each of two distances from the forest edge, 7.5 and 12.5 m (Fig. 2). Traps were placed on December 15, 1989, after clearing was completed.

Seed identification and size classes

Species were assigned to one of four size categories based on the average length (L) and width (W, longest axis perpendicular to L) of a sample of their diaspores (hereafter referred to as "seeds," although associated structures, such as wings of wind-dispersed fruits, were included.) "Large" seeds had W > 5 mm, "medium" had W < 5 mm but >1 mm, "small" seeds had W < 1 mm and $L \times W > 0.60$ mm², and "very small" seeds had $L \times W < 0.60$ mm². These criteria were used after trials revealed that seeds with W > 1 mm never passed through a 1-mm mesh, "small" seeds had moderate rates of passage (4–72 %), and "very small" seeds nearly always passed (80–100 %), unless they were imbedded in excrement.

With the exception of the first year's seed rain in strip 1, we did not aim to quantify "very small" seeds, and therefore only searched for seeds in material that did not pass a 1-mm mesh. However, "very small" seeds were encountered in this material, verifying the presence of additional species in the trap. Therefore, these seeds were identified and included in analyses of numbers of species. "Very small" seeds are excluded from all analyses of seed numbers.

We also quantified the seed rain of "large" seeds in year 4 after clearing. Traps were re-installed in their previous locations, and inspected weekly for 1 year beginning September 16, 1992 (40 months after clearing strip 1 and 34 months after clearing strip 2).

Because we were primarily interested in seeds that potentially could colonize sites not already occupied by conspecifics, we distinguished seeds likely to have fallen directly below the parent plant from those that were truly dispersed. For each trap, we considered seeds "fallen" if they belonged to a species fruiting above the trap or with >4 intact mature fruits or >4 intact immature fruits recovered in that trap. Otherwise, seeds were considered "dispersed." Except where noted, analyses of numbers of seeds from strip 1 are limited to "dispersed" seeds. Only one species (an unidentified Dilleniaceae liana) contributed "fallen" seeds larger than "very small" to strip 2, and these were not excluded from analyses. "Fallen" seeds are included in analyses of numbers of species.

Taxa with > 10 seeds in traps in and near strip 1 or > 5 seeds in traps in strip 2 over the 2 years of trapping were categorized as "near" or "far" seed sources based on whether there was at least one fruiting individual < 15 m from the strip, including plants within the strip that survived the cut. This determination was based on searches for flowering and fruiting plants at approximately 3-week intervals. The ruderal herb *Phytolacca rivinoides* was categorized as "near" since seeds



Fig. 2 Diagram of a logged strip $(30 \times 150 \text{ m})$ showing regeneration plots and location of seed traps. *Squares* indicate sites where seed traps were placed in both strips and *circles* indicate sites where traps were placed only in strip 1. Two additional columns of 16 seed traps each were placed in the forest near strip 1; one column 25 m west of the strip and the other 25 m east of the strip. Of the twenty 15×15 m plots in each strip, eight (indicated by *asterisks*) were censused for seedling regeneration

appeared in traps about the time that individuals within the strips began fruiting.

Identification of dispersal agents

Dispersal agents were determined for species using our own field data wherever possible (Appendix 1 of Supplementary Material). Specifically, we obtained fecal samples of birds and bats captured along the edge of both strips and in nearby habitats using nylon mist-nets, and matched seeds in feces with seeds in traps and the reference collection (Gorchov et al. 1995). Species were considered wind-dispersed if their diaspores contained wings or plumes or if small seeds dispersed passively from capsules that remained on the plant. For species where we lacked our own dispersal data, we used published data for the same tree species. For species for which we could find no literature on dispersal, we used published data for congeneric trees. For those trees only identified to genus level, we used the literature for the genus.

Because some S seeds and most VS seeds passed through the mesh, counts of small-seeded species are

underrepresented in the seed trap data. Because these species are bat-, bird-, or wind-dispersed (Appendix 1 of Supplementary Material), these dispersal modes are underrepresented, but there should be no spatial bias because traps were identical.

Recruitment studies

We censused all trees > 2 m on eight 15×15 -m plots (Fig. 2) six different times in each strip. To distinguish advance regeneration from recruits from seed, we marked every stump and stump sprout in censuses following felling. The analyses reported in this manuscript are limited to recruits from seed, which accounted for most of the regeneration (81 % of strip 1 and 76 % of strip 2 stems in the most recent census, Rondon et al. (2009)). Census years for strip 1 were 1990, 1992, 1993, 1996, 2000, and 2004; they were the same for strip 2 except the first census was 1991 and the last was done in 2005. Trees were identified using Gentry (1993) and Spichiger et al. (1989, 1990). Voucher specimens of difficult taxa were brought for comparison to Missouri Botanical Garden (MOBOT). Vouchers were deposited at the CIJH herbarium, AMAZ, and MU. Some trees could only be identified to the genus level, and a few only to family.

Early regeneration in these strips was dominated by pioneer trees, particularly Cecropia spp., Alchornea triplinervia, and several species of Melastomataceae (Gorchov et al. 1993). [Nomenclature for trees follows Spichiger et al. (1989, 1990), except we treat Cecropiaceae as a family distinct from Moraceae. Nomenclature for taxa other than trees follows Brako and Zarucchi (1993)]. A silvicultural thinning was carried out in 1996 in portions of each strip that included half of the plots (details in Dolanc et al. 2003); this involved girdling all *Cecropia* spp. stems as well as trees > 10 m of A. triplinervia and Melastomataceae. While thinning increased diameter growth increments of other trees, it did not affect their survival (Dolanc et al. 2003), and by the last census (2004/2005) its effects on composition were modest (Rondon et al. 2009). Thinned plots did not differ significantly from control plots in the distance-from-edge patterns of trees of different dispersal modes, so they were pooled for analysis.

At the last census, species richness of large (>7.5 cm diameter at breast height, dbh) trees had reached 50 % of its pre-clearing value, but pioneer trees still accounted for the majority of large stems and basal area on the strips (Rondon et al. 2009).

Here we analyze the composition of trees that recruited from seed after clearing and survived to the last census (2004 in strip 1, 2005 in strip 2). Each tree > 2 m was assigned to a "cohort" (based on the census when it first reached 2 m in height), a location [edge (E), intermediate (I), or center (C)], and a dispersal mode. Location refers to distance from the forest edge: E: 0-5 m, I: 5-10 m, and C: 10-15 m from the edge. Dispersal mode for each tree taxon followed methods described above for seeds, and coded as wind (W), bird [A (Aves)], bat [C (Chiroptera)], and nonvolant mammal (M). A few taxa were gravity-dispersed, or could not be assigned based on incomplete identification or literature; these were dropped from all recruit analyses. Tree taxa dispersed by multiple agents were given combined codes (Appendix 1 of Supplementary Material), but for analyses were assigned to the dispersal mode expected to be most likely to disperse seeds into newly cleared strips, based on Gorchov et al. (1993). Specifically, taxa for which bats were one of the dispersers were assigned to 'C', and any other taxa for which birds were one of the dispersers were assigned to 'A.' Most of the species dispersed by nonvolant mammals (M) had fleshy fruits (as did all seeds dispersed by birds and bats), with primates and other arboreal mammals being the predominant dispersers. However, some M species had dry fruits that were dispersed by terrestrial rodents; these seeds would be underrepresented in our traps.

Statistical analyses

The response used in this analysis was the total tree counts summed over plots within each strip. The factors of interest were location (E, I, C), cohort, dispersal mode (W, C, A, and M), and (in strip 2 only) cut method (clear cut; deferment cut). We did not include "species" or "taxa" as a factor in the models due to the large number of tree taxa in the data set (see "Results" section) and the fact that in each strip most species were represented by just one or a few trees. Because somewhat fewer trees recruited in 1992 and 1993 than in the other census years, these were combined to create the 92/93 cohort. Thus, for strip 1 the levels of cohort were 1990, 1992/1993, 2000, and 2004, while for strip 2 they were 1991, 1992/1993, 2000, and 2005. Separate analyses were done for each strip, because only strip 2 had different cut methods.

General linear models were used to investigate the main and interactive effects of location, cohorts, dispersal modes (DM), and cut method (CM) on mean tree count using SAS software, Version 9.2 of the SAS System for Windows (SAS Institute Inc., Cary, NC, USA). Nonsignificant ($\alpha = 0.05$) effects were dropped from the analysis. The final models, with the tests for the effects, for strips 1 and 2 can be found in Tables 2 and 3, respectively. Significant effects were further investigated using Bonferroni multiple comparisons of the least squares means.

Results

Seed dispersal

Strip 1

Ninety-six taxa had > 10 seeds recovered in traps in and near strip 1 (Appendix 1 of Supplementary Material); 54 % of these were identified to species. Of the 96 taxa, 57

28 were considered bird-dispersed, 19 bat-dispersed, and 15 wind-dispersed; many of the remainder were dispersed by more than one dispersal agent (e.g., six species were dispersed by birds and bats). While tentative assignments were made for some of the species (Appendix 1 of Supplementary Material), these were not used in the dispersal mode analyses reported below. Analyses did include species with <10 seeds in traps, however. Only two species (accounting for <0.03 % of dispersed seeds strip 1 in year 1 and <0.05 % in year 2) were dispersed only by nonvolant mammals, so this category was not used for analysis of seed deposition.

In each of the first 2 years after logging, the average species richness of seeds per trap declined from the forest to the edge to the strip interior (year 1 results in Gorchov et al. 1993; year 2 in Fig. 3). Spatial patterns differed for the three major dispersal modes; in each year the number of bird-dispersed species declined much more sharply from forest to strip than did the numbers of bat- or wind-dispersed species.

The total number of seeds dispersed into seed traps each year decreased from the forest to the edge to the interior of strip 1 (Table 1). For each of the first 2 years, bird-dispersed seeds declined in number more steeply from forest to edge to strip than did bat- or wind-dispersed seeds (Fig. 4). The high density of bat-dispersed seeds in the center during the second year was mostly due (63 %) to one species, *Cecropia ficifolia*, with two of the 32 center traps accounting for 77 % of the *C. ficifolia* seeds.

Very few seeds of taxa dispersed by nonvolant mammals reached the strips. In general, these trees have large seeds (Hammond et al. 1996), and the proportion of seeds dispersed into traps in or near strip 1 (excluding "very small" seeds) that were "large" was only 2.4 % in year 1 and 2.7 % in year 2 (Table 1). The number of large seeds dispersed into traps was somewhat lower in year 4 than in the first 2 years, although the number of seeds dispersed to traps within the strip was similar to that in year 2 (Table 1). More large seeds were dispersed





Table 1 The numbers of dispersed and fallen seeds in each size class (see "Methods" section) in strip 1 seed traps in the first, second, and fourth years after clearing

| Year | Seed size | Forest | | Edge | | Intermediate | | Center | |
|--------|-------------------------|-----------|--------|-----------|--------|--------------|--------|-----------|--------|
| | | Dispersed | Fallen | Dispersed | Fallen | Dispersed | Fallen | Dispersed | Fallen |
| Year 1 | Large | 184 | 145 | 54 | 361 | 13 | 46 | 7 | 0 |
| | Medium | 2,347 | 4,315 | 1,147 | 840 | 412 | 35 | 464 | 3,929 |
| | Small | 3,745 | 0 | 1,418 | 28,058 | 608 | 0 | 577 | 0 |
| | Very small | 20,010 | 14,035 | 5,284 | 1,716 | 1,569 | 0 | 756 | 0 |
| Year 2 | Large | 98 | 155 | 42 | 330 | 35 | 60 | 34 | 3 |
| | Medium | 1,773 | 7,911 | 877 | 352 | 264 | 6 | 506 | 3,195 |
| | Small | 661 | 0 | 611 | 34,044 | 1,006 | 0 | 1,750 | 0 |
| | Very small ^a | 893 | 10,366 | 531 | 127 | 629 | 0 | 1,066 | 0 |
| Year 4 | Large | 42 | 0 | 76 | 128 | 15 | 92 | 21 | 0 |

See "Methods" for explanation of forest, edge, intermediate, and center locations

^aVery small seeds were underestimated in year 2 because seed trap contents were sieved before inspection



Fig. 4 Mean number of seeds per trap (+SE) of all seeds and seeds dispersed by birds, bats, and wind at each location in strip 1, **a** year 1 and **b** year 2

into the strip interior in years 2 and 4 compared to year 1 (Table 1).

Strip 2

In strip 2, during the first year after clearing the species richness of seeds reaching traps was influenced by felling treatment and proximity to the forest edge: traps 7.5 m from the edge in the deferment-cut half had nearly double the species as traps 12.5 m from the edge or in the clear-cut half (not shown). In the second year, no such pattern was apparent.

The number of seeds per trap in strip 2 followed similar patterns to the species richness of seeds. In the first year, traps in the deferment-cut half that were closer (7.5 m) to the forest edge had more seeds than those in the other locations (Fig. 5a). In the second year, there was a tendency for seed density to be greater in the deferment-cut half and closer to the forest (Fig. 5b).

Dispersal from near versus far seed sources

For each of the two strips, we were able to estimate the minimum proportion of seeds originating from plants >15 m away from the strip/forest edge (hereafter "far"). Of the 100 species with >10 dispersed seeds in strip 1 traps, 49 had fruiting individuals within 15 m, 26 did not, and we are uncertain for the remaining 25. At least 54 % of dispersed seeds reaching strip 1 originated >15 m from the strip in the first year after clearing (Appendix 2 of Supplementary Material), with more reaching the edges of the strip than the interior. The following year, the proportion of seeds from "far" sources increased to >70.7 %, due largely to the C. ficifolia seeds reaching two of the center traps. If "fallen" seeds are included in the total, then the minimum estimates of seeds originating far from the strip drop to 6.7 % (year 1) and 8.3 % (year 2). For strip 2, of the 38 species with >5 seeds in traps, 15 had fruiting individuals within 15 m, 21 did not, and we are uncertain for the remaining 2. In the first year, >57 % of the seeds deposited in the clear-cut half and >54 % of those in the deferment-cut half originated > 15 m from strip 2. In the second year, the actual number of such "far" seeds increased in both halves, but their proportion increased only in the clear-cut half (to >71 %); in the deferment-cut half the proportion declined to > 31 %.



Fig. 5 Mean number of seeds per trap (+SE) at two different distances from the forest edge in the deferment-cut (south) half and the clear-cut (north) half of strip 2 in **a** year 1 and **b** year 2

Tree recruitment

While trees from over 184 genera were present in the final census of recruits from seed (Appendix 1 of Supplementary Material), the taxa that were most common were (in order) *Protium* spp., *Inga* spp., *A. triplinervia*, *Miconia phaeophylla*, *Virola* spp., *Ladenbergia magnifolia*, *Palicourea punicea*, *Guarea* spp., *Cecropia distachya*, *Pourouma* spp., and *Mabea riedelli*.

Strip 1

For strip 1, a total of 1,096 trees were analyzed and the final model (Table 2) fit very well, with 96.8 % of the variation in tree count explained by the included variables. As mentioned in the "Methods" section, the three-way interaction associated with testing the Schupp et al. (1989) model, cohort \times location \times dispersal mode, was not significant. Location \times dispersal mode was also not significant (Table 2).

The other two two-way interactions were significant. Cohort × dispersal mode was the more highly significant of these interactions (p < 0.0001, Table 2). In the first cohort, species dispersed by birds were more numerous than those dispersed by other agents, whereas in the later cohorts, species dispersed by nonvolant mammals

 Table 2 Final GLM model for tree recruits in strip 1 alive at the last census (2004)

| Source | df | Type III S | S Mean squar | e F value | p > F |
|----------------------------|----|------------|--------------|-----------|----------|
| Location | 2 | 9.500 | 4.750 | 0.22 | 0.8045 |
| Cohort | 3 | 4,592.063 | 1,530.688 | 70.74 | < 0.0001 |
| Dispersal mode | 3 | 8,811.896 | 2,937.299 | 135.74 | < 0.0001 |
| $Location \times cohort$ | 6 | 524.500 | 87.417 | 4.04 | 0.0061 |
| Cohort × dispersal mode | 9 | 1,889.021 | 209.891 | 9.7 | < 0.0001 |



Fig. 6 The number of surviving trees from each cohort for strip 1, stratified by seed dispersal mode. *NV* nonvolant

were most numerous (Fig. 6). Bat-dispersed and winddispersed trees were less numerous, and declined in frequency from early cohorts to later cohorts (Fig. 6).

The significant location \times cohort interaction (p = 0.0061, Table 2) was due to a high number of first-year recruits that were located in the center 5 m of the strip. In subsequent cohorts, similar number of recruits were in each location.

Strip 2

For strip 2, a total of 1,009 trees were analyzed, and the final model (Table 3) fit very well, with 89.6 % of the variation in tree count explained by the included variables. The three-way interaction cohort × location × dispersal mode, was not significant. Of the three-way interactions, only cohort × dispersal mode × cut method was significant (p = 0.0297). To explore this three-way interaction in a manner that facilitated comparison with strip 1, we examined each of the two cut methods (deferment cut, clear-cut) separately.

In the clear-cut half of strip 2, the final model explained 87.9 % of the variation, and the only interaction retained was cohort × dispersal mode (Table 4). This interaction appears attributed to distinct patterns for wind- and mammal-dispersed trees. While bird- and bat-dispersed trees were progressively less numerous in sequential cohorts, there was a relatively large number

| Source | df | Type III SS | Mean square | F value | p > F |
|--|----|-------------|-------------|---------|----------|
| Location | 2 | 15.896 | 7.948 | 0.67 | 0.5181 |
| Dispersal mode | 3 | 2,318.365 | 772.788 | 64.83 | < 0.0001 |
| Cohort | 3 | 1,392.281 | 464.094 | 38.93 | < 0.0001 |
| Cut method | 1 | 21.094 | 21.094 | 1.77 | 0.1897 |
| Location \times dispersal mode | 6 | 168.604 | 28.101 | 2.36 | 0.0447 |
| Cohort \times dispersal mode | 9 | 551.260 | 61.251 | 5.14 | < 0.0001 |
| Location × cohort | 6 | 56.438 | 9.406 | 0.79 | 0.5829 |
| Location \times cut method | 2 | 13.563 | 6.781 | 0.57 | 0.5699 |
| Dispersal mode \times cut method | 3 | 18.365 | 6.122 | 0.51 | 0.6749 |
| $Cohort \times cut method$ | 3 | 137.281 | 45.760 | 3.84 | 0.0153 |
| Cohort \times dispersal mode \times cut method | 9 | 248.427 | 27.603 | 2.32 | 0.0297 |

Table 4 Final GLM for tree recruits in clear-cut half of strip 2

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| Source | df | Type III SS | Mean square | F value | p > F |
|--------------------------------------|----|-------------|-------------|---------|----------|
| Location | 2 | 21.292 | 10.646 | 0.91 | 0.4124 |
| Cohort | 3 | 796.500 | 265.500 | 22.75 | < 0.0001 |
| Dispersal mode | 3 | 1,204.167 | 401.389 | 34.4 | < 0.0001 |
| $\dot{Cohort} \times dispersal mode$ | 9 | 523.667 | 58.185 | 4.99 | 0.0004 |



Fig. 7 For strip 2 clear-cut half (a) and deferment cut half (b), the number of surviving trees from each cohort, stratified by seed dispersal mode

of wind-dispersed trees in the second cohort (1992/1993) and of mammal-dispersed trees in the second and third (2000) cohorts (Fig. 7a).

In the deferment cut half of strip 2, 90.2 % of the variation in tree count was explained by the final model (Table 5). Two interactions were significant and retained in this final model. The cohort × dispersal mode interaction was significant, as it was for the clear-cut half and for strip 1, but in this case it appeared attributable to the last cohort (2005) having relatively more bat-dispersed and fewer mammal-dispersed trees than the other cohorts (Fig. 7b). The significant location × dispersal mode interaction appears attributable to the central part of the strip having relatively more trees of bird-dispersed species and fewer trees of mammal-dispersed species than the other portions of the strip (Fig. 8).

Discussion

Seed deposition

Our finding that seed input into recently logged strips was much lower than nearby forest understory contrasts with studies of seed rain into treefall gaps, which found seed input quantitatively similar to that in understory (Augspurger and Franson 1988; Loiselle et al. 1996; Martini and dos Santos 2007). The difference may be due to the larger size and simpler vegetation structure of strips compared to gaps. Another likely cause of the difference is lower seed production within the strips than within gaps, due to the paucity of advance regeneration.

Although many of the seeds reaching the strips were of taxa represented by fruiting plants along or near the

Table 5 Final GLM for tree recruits in deferment cut half of strip 2

| Source | df | Type III SS | Mean square | F value | p > F |
|----------------------------------|----|-------------|-------------|---------|----------|
| Location | 2 | 8.167 | 4.083 | 0.38 | 0.6857 |
| Cohort | 3 | 733.063 | 244.354 | 22.94 | < 0.0001 |
| Dispersal mode | 3 | 1,132.563 | 377.521 | 35.44 | < 0.0001 |
| Location \times dispersal mode | 6 | 191.500 | 31.917 | 3 | 0.0249 |
| Cohort × dispersal mode | 9 | 276.021 | 30.669 | 2.88 | 0.0186 |



Fig. 8 For the deferment cut half of strip 2, the number of trees in each 5 m wide location, stratified by seed dispersal mode

edge, the majority were from more distant sources, highlighting the importance of seed-dispersal vectors in bringing seeds to the strips. Other studies of seed rain did not separately quantify seeds originating in plants closest to traps versus those further away, as we did, but note that local seed production by pioneers dominates seed traps (Martini and dos Santos 2007).

Our finding that wind-dispersed seeds showed less of a decline from forest to strip than bird-dispersed seeds is similar to a study of recruitment from soil "seed traps" in Costa Rican forest, where wind-dispersed seeds were associated with gaps rather than understory sites, in contrast to animal-dispersed seeds (Loiselle et al. 1996). In Brazilian Atlantic forest, there were fewer small animal-dispersed seeds, but similar numbers of seeds dispersed by wind and by medium-sized animals, in recent gaps compared to nearby forest understory (Martini and dos Santos 2007). In a dry-season study in Panama, deposition of wind-dispersed seeds was actually greater in gaps than in forest understory, while deposition of non-wind-dispersed seeds was lower (Augspurger and Franson 1988). Our results differ in that the input of wind-dispersed seeds was reduced in the strip, albeit less than was the input of animal-dispersed seeds.

Deposition of bat-dispersed seeds differed from birddispersed seeds; bat-dispersed seeds were more likely to be found in gap centers in the second year, as well as the first year (Gorchov et al. 1993) after clearing. Most other studies of seed dispersal in tropical forest have not distinguished bat-dispersed taxa from those dispersed by other animals, but those that did found similar patterns. Charles-Dominique (1986) found that gaps and open areas received seeds of pioneer plants only at night, attributed to bat-dispersal, whereas in forest understory and areas with sparse trees, most deposition was diurnal and attributed to birds. Similarly, nocturnal deposition of feces bearing *Muntingia calabura* seeds was skewed toward open savanna while diurnal deposition was greatest along a forest corridor (Thomas et al. 1988). Low input of bird-dispersed seeds into open habitats in and near forests is likely due to avoidance of these habitats by forest birds; for example, Johns (1991) documented that many bird species of Amazonian forest are not observed in the shrubby growth of abandoned fields.

Tree recruitment

The spatial patterns in recruitment of trees dispersed by different dispersal agents did not strongly parallel the patterns we found in seed dispersal in the first 2 years after clearing. For example, bat- and wind-dispersed trees did not dominate in the center of the strips, with mammal-dispersed taxa dominating the edges, as would be expected based on seed dispersal during the first 2 years. Only in the deferment cut did we seed birddispersed taxa predominating in the center and mammal-dispersed taxa predominating near the edge.

A weak correspondence between spatial patterns of seed dispersal and tree recruitment could be due to many factors (Schupp and Fuentes 1995). Each of the dispersal modes comprised many different taxa, which no doubt differ in patterns of seed deposition and recruitment along environmental gradients, in this case the forest edge-to-center gradient. Our focus was on testing the broad patterns among dispersal modes, as done by Augspurger and Franson (1988), Schupp et al. (1989), and Loiselle et al. (1996), rather than spatial patterns of individual species, or whether individual species showed correspondence between deposition and recruitment patterns. At any rate, the low sample size of most species precluded analysis at the species level.

The forest edge-to-center gradient involves not only light, and hence interspecific differences in shade tolerance, but also differences in pathogen attack and seed predation (Schupp et al. 1989). In our system, seed predation on nonvolant mammal-dispersed *Macoubea guianensis* was lower in the strips than near source trees in the forest, but predation on bat- and nonvolant mammal-dispersed *Pouteria* sp. was higher (Notman et al. 1996). In this study, an additional factor affecting the correspondence between spatial patterns of seeds and recruits relates to our analysis of only those recruits that were alive 15 years after strips were cleared. While this is the relevant subset for analyses when one is interested in the composition of the regenerating forest, we note that most trees in the earlier cohorts were no longer alive at this last census. These non-persisting recruits were primarily short-lived, shade-intolerant trees, particularly *Cecropia* spp., which are bat-dispersed (Gorchov et al. 1993).

Seed dispersal is not the only source of new recruits following disturbance, but it is the most important source following clear-cutting in the Peruvian Amazon (Gorchov et al. 1993; Rondon et al. 2009), justifying our focus on recruits from seed. Advance regeneration is less important in logged clearings than it is in treefall gaps (Dickinson et al. 2000). Although recruits from the seed bank predominate in certain situations [as in new treefall gaps in the Columbian Amazon, where they outnumbered recruits from the seed (Castillo and Stevenson 2010)], in our study the seed rain was much more important; only one of the trees common in the early regeneration, *Cecropia membranacea*, was present in the seed bank (Gorchov et al. 1993).

Temporal patterns in the relative importance of different dispersal modes to tree recruitment did not exactly match what would be expected from Schupp et al. (1989). Note that "recruitment" in our study was defined as reaching 2 m in height, so slower-growing taxa would be counted in a later cohort than fastergrowing taxa. Schupp et al.'s prediction of reduced representation of wind-dispersed trees over time was seen in strip 1, where later cohorts had lower proportions of wind-dispersed trees, but in the clear-cut part of strip 2 there was no clear pattern, and in the deferment cut, wind-dispersed trees were best represented in the second cohort. While Schupp et al. expect very low representation of large-seeded animal-dispersed trees in new or maturing gaps, we found that trees dispersed by nonvolant mammals, which generally have larger seeds than the other dispersal modes, were common in all cohorts in both strips; this category was the most common in strip 1 and the second most common in strip 2. These mammal-dispersed trees were relatively uncommon in the earliest cohort in the clearcuts, but not in the deferment cut, consistent with our finding of low input of large seeds into cleared strips in the first year after felling, presumably because the open habitat discouraged mammal activity. At this study site, mammals may have been particularly averse to open areas, and at low abundance, due to hunting pressure.

The greater importance of later cohorts in the deferment cut half of strip 2, compared to the clear-cut half of strip 2 and the clear-cut strip, is likely due to slower growth of trees to the 2 m threshold in shade. Slower growth in shade also likely explains the later recruitment along the edges than in the center of strip 1.

An important caveat in this study is that our assignment of tree taxa to seed dispersal modes did not capture the complexity of seed dispersal. Some trees are dispersed by animal species in distinct taxa, such as birds and bats (Gorchov et al. 1995), and it is not possible to infer which taxon is most important in a particular place and time without a focused study on that tree species. Our decision to re-classify tree taxa based on the most effective taxon at dispersing seeds into strips (Gorchov et al. 1993) facilitated detection of broad patterns, but it likely obscured other relationships that would require more focused study.

Management implications

In order for strip clear-cutting (or other high-volume extraction systems of timber management) to be economically sustainable, commercial species must be well represented in the regenerating stand (Rondon et al. 2009). Commercial timber species in tropical America have larger seeds than non-commercial species, and most are dispersed by mammals, rather than birds or wind (Hammond et al. 1996). These mammal-dispersed timber trees are primarily dispersed by primates and other nonvolant mammals rather than bats. In our study site, sufficient seeds of nonvolant mammal-dispersed trees were dispersed into logged strips so that these comprised a large fraction of the recruits. This highlights the importance of conserving viable populations of these mammals to the sustainable forest management. Several recent studies have shown that tropical forests subjected to hunting have lower populations of seed-dispersing nonvolant mammals and inferior dispersal or recruitment of mammal-dispersed taxa (Beckman and Mueller-Landau 2007; Brodie et al. 2009; Holbrook and Loiselle 2009; Nuñez-Iturri and Howe 2007). Maintaining high populations of seed-dispersing mammals is particularly challenging because hunting typically increases when forests are opened to logging (Robinson et al. 1999).

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