Regaining Landscape Connectivity Through the Restoration of Seed Dispersal Processes

BY

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THESIS

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I am especially grateful to my family and friends. Parents, husband, sisters, aunts and

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CONTRIBUTION OF AUTHORS

Chapter 1 is comparative evaluation of dispersal and establishment limitations that occur in the primary forest and secondary forest compared to recently abandoned pastures. My research advisor, Dr. Henry F. Howe and Dr. Cristina Martínez-Garza conceived and designed the experiment. I conducted the research, developing the research questions, collecting the data analyzing it and writing the manuscript. Dr. Henry F. Howe and Dr. Cristina Martínez-Garza contributed to the writing of the manuscript.

Chapter 2 proposes indices to better understand the dynamics of seeds and seedlings. I am the primary author of this chapter and major driver of the research. I proposed the research idea, collected the data, coordinated the collaborators, analyzed the data with the proposed formulas and wrote the manuscript. Three mathematicians, Emiliano Cruz-León, Rita Jiménez-Rolland, Cesar Lozano-Huerta, collaborated in developing the indices and formulas. B.Sc. Yuliana Urincho-Pantaleón contributed with the seed fall data. Dr. Henry F. Howe and Dr. Cristina Martínez-Garza contributed to the writing of the manuscript. The work from my first two chapters will be submitted for publication.

Chapter 3 represents a published manuscript (de la Peña-Domene, M., Martínez-Garza, C. & Howe, H.F. 2013. Early recruitment dynamics in tropical restoration. *Ecological Applications,* 23, 1124-1134). Dr. Henry F. Howe and Dr. Cristina Martínez-Garza conceived and designed the experiment. I was the primary author; I was in charge of collecting the seedling recruitment data since 2007, I analyzed the data with help from Dr. Cristina Martínez-Garza and wrote the manuscript in collaboration with Dr. Henry F. Howe and Dr. Cristina Martínez-Garza.

Chapter 4 is a published manuscript (de la Peña-Domene, M., Martínez-Garza, C., Palmas-Pérez, S., Rivas-Alonso, E. & Howe, H.F. 2014. Roles of Birds and Bats in Early Tropical-Forest Restoration. *Plos One*, 9, e104656), where I was the primary author. M. Sc. Edith Rivas Alonso developed the hypothesis; I collected the data, and wrote the manuscript, the analysis were conducted by myself with the contribution of Sebastián Palmas-Pérez. Dr. Henry F. Howe and Dr. Cristina Martínez-Garza conceived and designed the experiments and contributed writing the manuscript, and analyzing data.

Finally, for Chapter 5, I conducted the research from the data collection to the development of the manuscript. Dr. Emily Minor provided support conceiving the manuscript and analyzing data. Both Dr. Henry F. Howe and Dr. Emily Minor contributed to write the manuscript, which will be submitted for publication shortly.

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SUMMARY

Forests around the world are under pressure to deliver economic, social, and environmental services. Conventional agriculture threatens biodiversity; however, many families depend on it for their livelihoods and global demand for food is increasing. It is an immense challenge to meet these two objectives (food production and biodiversity conservation). One alternative to conventional food production is the practice of planting mixed-species patches of native vegetation. For my dissertation, I evaluated how mixed plantings help to maintain countryside biodiversity and landscape connectivity in human-dominated landscapes. This study was conducted in Los Tuxtlas, Mexico, the northernmost remnant of tropical rainforest in the American continent. Los Tuxtlas is a biodiversity hotspot facing severe fragmentation (87% of its original forest area is now cattle pasture). Regaining connectivity between forest fragments through a network of vegetation patches that work as stepping-stones can decrease the pressure from deforestation and the effects of fragmentation, thereby maintaining biodiversity and many ecosystem services. It can also sustain food production in the long term. In a series of studies at this site, I first explored how dispersal and establishment limitations are acting on three habitat types: primary forest, secondary forest and pasture lands. Next, I examined the effect of mixed-species plantings on accelerating succession from pasture to forest. Finally, I assessed the role of experimental restoration plots on the conservation of an endemic, vulnerable tree species.

Dispersal and establishment limitations play a crucial role in determining the species assemblage of the resulting plant community. In this study, I evaluated existing measures and proposed new metrics to assess seed dispersal and seedling establishment limitations

in three different habitats (primary forest, secondary forest and pasture). Primary and secondary forest show different dynamics of dispersed seeds and established recruits; yet in pastures, limitations are more severe than in either of these forest types. Few seeds actually arrive into pastures away from the forest edge, and even fewer become established recruits.

Given the severe limitations, I then experimentally evaluated the potential of mixed-species plantings embedded in pastures to overcome dispersal and establishment limitation and accelerate succession back to forest. Seedling recruitment increased greatly under mixed-tree plantings of wind-dispersed and animal-dispersed species within the first five years. Moreover, seedlings of animal-dispersed later successional species showed a greater increase in number of species and individuals than all pioneer species or wind-dispersed later successional species. This indicates that forest succession under mixed-species plantings promote recovery of species diversity at a higher rate than natural succession.

Frugivorous bats and birds are known to contribute to forest succession through seed dispersal in different ways. I evaluated the contribution of bats and birds to effective dispersal, measured as the number of established seedlings of a given species. Seedlings of later successional trees that were dispersed by birds established at a much higher rate than pioneers and bat-dispersed later successional trees.

The decline in abundance and distribution of larger animals can eventually lead to the decline of large-seeded trees. I studied how planted plots at a landscape level decreased the costs of dispersal agents for *Ocotea uxpanapana*, an endemic, vulnerable and large-seeded tree species. Planted plots effectively recovered habitat for these large-seeded

species even though plots were surrounded by a matrix of active cattle pastures. Planting

networks of high diversity stepping-stones could be used as a conservation tool for large-

seeded tree species.

INTRODUCTION

Many forests around the world are facing unsuitable levels of pressure to deliver

economic, social, and environmental services (Paquette and Messier 2010). Tropical

forests have the highest biodiversity of all terrestrial ecosystems (Turner 1996, Dirzo 2001).

However, more than half of the world's tropical forests have been lost to agriculture and

other uses (Bryant et al. 1997). Conventional agricultural activities pose the greatest

extinction threat to bird extinction, the best known taxon (Green et al. 2005), and evidently

for other animal and plant groups as well. While agriculture has been described as the

antithesis of biodiversity (Perfecto and Vandermeer 2010) world demand for food is

increasing (Green et al. 2005) and with it the need to come up with viable solutions that

can meet these two objectives (food production and biodiversity conservation).

Throughout Latin America vast expanses of tropical rain forests are converted to pasture.

This leaves highly fragmented mosaics of farms, forest remnants, and small habitat

patches (Houghton 1994, Ojima et al. 1994, Montagnini and Jordan 2005) where regional

extinction will occur if there is no inter-fragment migration to balance local extinction

(Vandermeer and Perfecto 2007). Ecosystem services are also jeopardized with land-cover

changes. The capacity of ecosystems to sustain food production, maintain fresh water and

forest resources is reduced under some human land-use practices (Foley et al. 2005).

Together, croplands and pastures are among the largest terrestrial biomes on the planet,

occupying close to 40% of land surface (Ramankutty and Foley 1999, Asner et al. 2004,

Foley et al. 2005). Conservation efforts focused solely on protecting pristine remnants of

forest are of great importance, yet they overlook the potential contribution of prevalent

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agricultural landscapes to biodiversity conservation over tens of millions of square kilometers, particularly in the tropics.

Extensive cattle production is deeply rooted in the culture and rural economies of most Latin American countries; hence, it is not realistic to assume that the cattle economy will disappear while it is profitable. However, due to the huge area occupied by conventional cattle ranches and their social and economic importance, Perfecto (2010) argues that the agricultural matrix is perhaps the most important habitat on which conservation efforts should focus. Nevertheless, conventional grazing systems are in urgent need of transformation in order to become more productive and environmentally friendly (Murgueitio et al. 2011). As an alternative to conventional food production, high quality matrix in which patches of high diversity of native vegetation that can persist along with small-scale sustainable farming systems (Perfecto and Vandermeer 2010). Here, we test how countryside diversity and connectivity in human-dominated landscapes is maintained as an integrated landscape scheme.

Unassisted succession after grazing is often slow due to poor seed rain (Martínez-Garza and González-Montagut 1999, Slocum 2001, Martínez-Garza et al. 2009). The vast majority of tropical rain forest plants are dispersed by animals (Frankie et al. 1974, among others, Howe 1977, Howe and Smallwood 1982), yet many potential dispersal agents avoid crossing open pastures (Schupp et al. 1989). Planting animal-dispersed trees accelerates tropical succession by attracting dispersal agents, and thus seeds carried from the forest (see Wunderle 1997, Lamb 1998, Zimmerman et al. 2000, Chazdon 2003, 2008). This practice potentially bypasses decades of low-diversity, often wind-dispersed, pioneer forests (Martínez-Garza and Howe 2003, de la Peña-Domene et al. 2013). A realistic

restoration goal in such landscapes is to facilitate dispersal processes that recover and maintain those subsets of animals and plants able to coexist with people – allowing connectivity among habitat remnants (Turner and T. Corlett 1996, Daily et al. 2001, Hughes et al. 2002, Vandermeer and Perfecto 2007). Such efforts potentially maintain genetic connectivity among trees in forest remnants through long-distance pollen exchange (Aldrich and Hamrick 1998, Kramer et al. 2008), and facilitate population movement via seed dispersal in response to climate or other environmental changes (Corlett 2011). Regaining connectivity within the agricultural landscape is a key component to combine food production with biodiversity conservation.

LITERATURE CITED

Aldrich, P. R., and J. L. Hamrick. 1998. Reproductive dominance of pasture trees in a fragmented tropical forest mosaic. Science 281:103-105.

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses and global change. Annual Review of Environment and Resources 29:261-299.

Bryant, D., D. Nielsen, L. Tangley, N. Sizer, M. Mirand, P. Brown, N. Johnson, A. Malk, and K. Miller. 1997. The last frontier forests: ecosystems and economies on the edge. What is the status of the world's remaining large, natural forest ecosystems? Forest Frontiers Initiative, Washington, D.C.

Corlett, R. T. 2011. Impacts of warming on tropical lowland rainforests. Trends in ecology & evolution (Personal edition) 26:606-613.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6:51-71.

Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458-1460.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica. Ecological Applications 11:1-13.

de la Peña-Domene, M., C. Martínez-Garza, and H. F. Howe. 2013. Early recruitment dynamics in tropical restoration. Ecological Applications 23:1124-1134.

Dirzo, R. 2001. Tropical forests. Pages 251-276 in O. Sala, F. S. Chapin, and E. Huber-Sannwald, editors. Global Biodiversity in a Changing Environment. Springer-Verlag, Nueva York.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global Consequences of Land Use. Science 309:570-574.

Frankie, G., W. , H. G. Baker, and P. A. Opler. 1974. Comparative Phenological Studies of Trees in Tropical Wet and Dry Forests in the Lowlands of Costa Rica. Journal of Ecology 62:881-919.

Green, R. E., S. J. Cornell, J. P. W. Scharlemann, and A. Balmford. 2005. Farming and the Fate of Wild Nature. Science 307:550-555.

Houghton, R. A. 1994. The worldwide extent of land-use change. Bioscience 44:305-313.

Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539-550.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 2002. Conservation of tropical forest birds in countryside habitats. Ecology Letters 5:121-129.

Kramer, A. T., J. L. Ison, M. V. Ashley, and H. H. F. 2008. The Paradox of Forest Fragmentation Genetics. Conservation Biology 22:878 - 885.

Lamb, D. 1998. Large-scale ecological restoration of degraded tropical forest lands: the potential role of timber plantations. Restoration Ecology 6:271-279.

Martínez-Garza, C., A. Flores-Palacios, M. De La Peña-Domene, and H. F. Howe. 2009. Seed rain in a tropical agricultural landscape. Journal of Tropical Ecology 25:541-550.

Martínez-Garza, C., and R. González-Montagut. 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecology 145:255-265.

Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. Journal of Applied Ecology 40:423-429.

Montagnini, F., and C. F. Jordan. 2005. Tropical Forest Ecology: The Basis For Conservation And Management. Springer Berlin Heidelberg New York, Netherlands.

Murgueitio, E., Z. Calle, F. Uribe, A. Calle, and B. Solorio. 2011. Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. Forest Ecology and Management 261:1654-1663.

Ojima, D. S., K. A. Galvin, and B. L. Turner. 1994. The Global Impact of Land-Use Change. Bioscience 44:300-304.

Paquette, A., and C. Messier. 2010. The role of plantations in managing the world's forests in the Anthropocene. Frontiers in Ecology and the Environment 8:27-34.

Perfecto, I., and J. Vandermeer. 2010. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. Proceedings of the National Academy of Sciences 107:5786-5791.

Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. Global Biogeochemical Cycles 13:997-1027.

Schupp, E. W., H. F. Howe, C. K. Augspurger, and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology 70:562-564.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology 82:2547-2559.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200-209.

Turner, I. M., and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology & Evolution 11:330-333.

Vandermeer, J., and I. Perfecto. 2007. The Agricultural Matrix and a Future Paradigm for Conservation. Conservation Biology 21:274-277.

Wunderle, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223-235.

Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology 8:350-360.

CHAPTER I

1. HABITAT DIFFERENCES IN DISPERSAL AND ESTABLISHMENT LIMITATION IN A TROPICAL AGRICULTURAL LANDSCAPE

Habitat differences in dispersal and establishment limitation in a tropical agricultural landscape

Marinés de la Peña-Domene, Cristina Martínez-Garza and Henry F. Howe

1.1 INTRODUCTION

Two critical barriers to plant regeneration and succession are seed and establishment limitation. Failure of seeds to reach a site strongly limits regeneration of many plant species (Wijdeven and Kuzee 2000). The presence of a plant species is potentially determined by the arrival of seeds to a suitable site, but seed arrival does not guarantee seed germination and seedling establishment (Clark et al. 2013, Reid and Holl 2013). A variety of environmental and biological factors filter seedling establishment. Some of these factors include soil fertility (Holl et al. 2003, Fine et al. 2004, Palmiotto et al. 2004), soil moisture (Engelbrecht et al. 2002) and seed and seedling predation by insects, pathogens or vertebrate animals (Janzen 1970, Howe and Smallwood 1982, Myster 2003). Moreover, in open pastures high temperature, low humidity and strong competition with grasses decouple seed arrival and seedling establishment and survival (Buschbacher 1986, Nepstad et al. 1991, Parrotta 1995). Accumulation of soil nutrients and higher humidity under tree canopies favor seedling recruitment (Rhoades et al. 1998). However, restricted light under tree canopies limits juvenile growth of some species more than others (Turner 2001, Kitajima 2002). In either open or shaded situations, competition with heterospecifics constrains some species more than others (Nepstad et al. 1991, Myster 2004). For some species there is little disparity between the fortunes of dispersed seeds and seedlings; for others, the disparity between seed arrival and actual recruitment is immense.

Seed size affects both dispersal and seedling survival in different habitats. Small-seeded species normally disperse more seeds (< 4 mm wide), but in open areas, they also have higher seed-predation rates (Nepstad et al. 1990, Nepstad et al. 1991, Jones et al. 2003, Myster 2003, García-Orth and Martínez-Ramos 2008), especially by ants and small rodents. Larger seeds are less susceptible to pathogens (Sork 1987, Brokaw and Scheiner 1989), they suffer lower predation rates in open areas. Additionally seedlings of species with large seeds are less susceptible to droughts and high temperatures than seedlings from smaller seeds (Nepstad et al. 1990, Kitajima 2002). Larger seeds in the Neotropics normally depend on animal vectors for dispersal, thereby overcoming what would otherwise be extreme dispersal limitation.

Habitat can play a large role by influencing seed arrival and by providing conditions that favor seedling establishment. Animal-dispersed seeds depend on the mobility of animals that select specific foraging areas while avoiding others, such as open fields (Guevara and Laborde 1993, Estrada and Coates-Estrada 2001, 2005, Laborde et al. 2008). Wind-dispersed species do not depend on animals, but wind currents normally do not carry large seeds long distances; most seeds end up no more than 10m from the forest edge (Martínez-Garza and González-Montagut 1999). Even inside the forest, wind dispersal is often inefficient because wind currents are blocked by standing vegetation(Nathan et al. 2008). If small seeds are dispersed frequently but have low survival and larger seeds have high survival but are not dispersed, all species potentially experience dispersal limitation.

Until recently, there has been no quantitative framework for distinguishing effects of seed-dispersal limitation (hereafter dispersal limitation) from limitation in establishment of seedlings (hereafter establishment limitation). Both are components of recruitment

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limitation. Muller-Landau and colleagues (2002) developed indices for dispersal and establishment limitation, based on the assumption that seed rain into seed traps can be compared with the emergence of seedlings on the forest floor near traps. These authors assumed that one seed of a species in a seed trap was sufficient to record presence of a species in seed rain, based on the notion that no more than one adult tree can occupy a limited (e.g., 1 m2) area. Here we extend what we term a "presence index" to accommodate the arrival of multiple seeds of a species in a trap, a "density-weighted index" that assumes seeds within a species vary in genotype, and that different species vary widely in viability and other factors that influence germination. We use both presence and density indices to quantify dispersal and establishment limitation in three different habitats of a tropical agricultural landscape. Our objective is to test the degrees of dispersal limitation and establishment limitation of tree species with data on both seed rain and seedling establishment in a mosaic of primary forest, secondary forest, and pasture lands.

1.2 METHODS

1.2.1 Study site and sampling

The Los Tuxtlas Biological Reserve (3,500 ha) is a lowland tropical rain forest in the state of Veracruz, southeast Mexico (description and botanical check-list in González Soriano et al. 1997). The habitat is lowland rain forest, with a mean annual temperature of 27° C and mean annual precipitation of 4,900 mm (Gonzalez-Soriano et al. 1997). Twenty-four fenced 30 x 30 m plots separated by 35 m of grazed pasture were arranged in a 3 x 8 grid facing the Gulf of Mexico (further details in de la Peña-Domene et al. 2013). Eight plots were planted with seedlings of animal-dispersed species, eight with seedlings of wind-

dispersed species, and eight left as fenced, unplanted controls. For the time frame of this study (12 months from 2007 to 2008), plantings did not contribute to seed rain because planted seedlings were 0.2-1 m (0.33 ± 0.2 m) tall by the end of the seed-rain sampling (see Martinez-Garza et al. 2013). No planted or recruited trees reproduced by the end of this study (June 2008).

Seed samples were collected from pasture and forest habitats. Each seed trap consisted of four 1-m poles of PVC supporting a 1-m^2 frame covered by a shade cloth net with a rock in the middle to prevent seed roll. Twelve seed traps in each forest habitat (primary and secondary within continuous forest) ca. 200 m from the forest edge were located at random in an area corresponding to three of the pasture plots (90 × 30 m). Four seed traps in each pasture plot were located at random, stratified by plot quarter, for a total of 96 seed traps, over a total area of 14,414 m^2 of recently-fenced pasture.

From January 2007 through February 2008, seed samples were collected monthly in pasture and twice a month in forest to avoid germination in the damper forest sites. Seeds were separated, counted and identified to species at the State University of Morelos (UAEM), Mexico. Seed identification was done using the herbarium at LTBS and reference collections from previous studies (Martínez-Garza et al. 2009). A sample of seeds of each species was preserved and photographed as a reference collection at UAEM.

Recruits were censused every four months from June 2007 to June 2008 in pasture, primary forest and secondary forest. Forest recruit samples were from 5m^2 next to each of 12 seed traps (i.e. 12 stations) in primary and 12 seed traps (12 stations) in secondary forest. As a preliminary test we employed EstimateS (Mao Tau; Colwell 2006; Figure 1.7.1) to evaluate species accumulation for seeds and seedlings. We used 12 seed traps and adjacent

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understory quadrats for each habitat to evaluate seedlings. Initial evaluation of seeds and

recruits reveled a vast difference in densities of seeds and recruits in the two forest types

as compared with pasture (Figure 1.7.1), indicating the need for a much larger sampling

area in pasture to detect both seed rain and seedling establishment of species. Hereafter

we limit our discussion to comparisons of subsets of species with both seed and seedling

samples.

Some seed rain and recruitment data overlap with Martínez-Garza *et al.* (2009) and Howe

et al. (2010). Martínez-Garza and colleagues evaluate seed rain with respect to habitat;

Howe and colleagues evaluate pasture seed rain and seedling recruitment with respect to

spatial and legacy factors, including proximity of forest edge, living pasture trees, stumps

of trees cut during site preparation, and living fences, as well as soil depth. Neither

attempted a formal comparison of dispersal and establishment limitation.

1.2.2 Calculations and Analysis

1.2.2.1 Presence indices

Presence indices for species with adequate samples were adapted from Muller-Landau et al.

(2002). We calculated dispersal (seed) limitation and establishment limitation as:

$$Dispersal(seed) \; limitation = \; 1 - \frac{a}{n}$$

$$Establishment \; limitation = \; 1 - \frac{r}{a^*}$$

Where *a* is the number of stations (seed trap with adjacent recruitment area) receiving

seeds of sp.1 in the study period, *a** corrects area by averaging recruitment area to

correspond to the area for seed rain (1m^2). Variable *n* is the total number of stations and *r*

as the number of stations where both seeds and seedlings of a species occurred. The indices for a given species range from 0 to 1, where zero represents no limitation and 1 indicates complete limitation. This can also read as a percentage from 0% to 100% limitation.

1.2.2.2 Density-weighted indices

Several factors must be taken into account when calculating establishment limitation of a species in a given habitat. The first most obvious factor is the ability of a species to disperse its seeds into the habitat, where seeds represent the colonization potential of a species. Dispersal limitation can be calculated operationally as the number of seed traps that were not reached by seeds of a given species (*sensu* Muller-Landau et al. 2002). What we call the *density-weighted indices* adjusts *presence indices* to accommodate multiple dispersal events of a species into the same area of each habitat. An argument for not considering seed densities into account in the formula is that only one tree can recruit and grow in a given m^2 (Muller-Landau et al. 2002). Yet, if more than one seedling of a species establishes and reaches the juvenile stage in 1 m^2, the probabilities of one surviving density-dependent or density-independent mortality are different than if one seedling of a species establishes.

Extending the *presence indices* to include densities of seed rain accounts for inter-specific competition, density-dependent seed predation, and other sources of density-independent mortality that might occur among seeds and seedlings (here less than 1 yr old juveniles). We considered the fraction of seeds and/or seedlings contributed by a particular species, relative to the total number of seeds or seedlings arriving at a sampling station. Given n, the total possible values of a were divided into two equal factors, one for the abundance of

seeds or seedlings and the other for the proportion of traps reached by seeds of a given species. For seed limitation, the density-weighted index is:

$$Dispersal\ seed\ limitation = 1 - \frac{\frac{s_i}{S} + \frac{a}{n^*}}{2}$$

Similarly, for establishment limitation, the density-weighted index is:

$$Establishment\ limitation = 1 - \frac{\frac{p_i}{P} + \frac{r}{a^*}}{2}$$

As in earlier formulations (Muller-Landau *et al*. 2002), factor a^* is the number of seed traps where sp.1 is present corrected by area, n^* is the total number of stations corrected by area, and r is the number of stations with both seed(s) and seedlings of sp.1. For seed abundance, factor s_i represents the number of seeds of sp.1 and S, the total number of seeds in all traps. Seedling abundances are represented by p_i as the number of recruits of sp.1 near traps where seeds of that species where present, and P is the total number of recruits.

Distributions of limitation values are highly skewed and not amenable to useful transformation, precluding presentation or analysis with parametric tools. For ease of visual inspection, we illustrate frequency distributions or box plots of medians and quartiles. Analyses include non-parametric Kruskal-Wallis tests of ranks, and the Wald-Wolfowitz runs test. Statistical tests were conducted in Statistica 7 (Statsoft, 2004). Species authorities and families follow Boyle et al. (2013) and Arroyo-Rodríguez et al. (2009).

1.3 RESULTS

1.3.1 Dispersal and establishment limitation in different habitats

Kruskal-Wallis one-way analysis of variance by ranks showed similar patterns of dispersal limitation among the habitats evaluated by both indices. Presence (Figure 1.7.2a), and density (Figure 1.7.2b) indices for dispersal limitation were higher in pastures than in either forest type and. Overall, the presence index ranked dispersal limitation higher in primary forest than secondary forest (P < 0.01) and pasture (P < 0.0001) than did the density-weighted index. The presence index for establishment did not differ by habitat (Figure 1.7.2c), with high but indistinguishable medians between 0.90 and 0.97. Density-weighted indices in establishment limitation differed by habitat, with higher median limitation in pasture than secondary forest (Figure 1.7.2d). In this case, the density-weighted index estimated less establishment limitation in secondary forests compared to pastures (P < 0.01).

1.3.2 Differences presented by the indices for each species in the three habitats

Presence and density indices for dispersal and establishment varied by species and habitat. A Wald Wolfowitz runs test showed significant differences among the indices across all habitats (Figure 1.7.3). In primary forest, the pattern of dispersal limitation revealed by both indices is similar for most species. Nevertheless, the density-weighted index estimated greater dispersal limitation for species with medium-sized seeds *Stemmadenia donnell-smithii, Chamaedorea alternans* and *Cupania glabra* and for the large-seeded *Nectandra ambigens*. Establishment limitation estimated by the presence indices were always high in primary forest (80-100%), but were much lower with the density-weighted index (50-70%), especially for larger-seeded species and some small-seeded species (around 70%). *Nectandra ambigens* varied from highest limitation using the

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presence index (> 90%) to moderate limitation (< 60%) using the density-weighted index (Figure 1.7.3).

Presence and density indices for dispersal limitation in secondary forest differed among species. Dispersal limitation was numerically higher when densities were included (Figure 1.7.4). Notably, establishment limitation was > 80% for all species using the presence index but as low as 40% using the density-weighted index (Figure 1.7.3).

In pastures, 10 out of 13 species showed extremely high dispersal limitation. Among the three least-limited species, *Cordia alliodora* surpassed 60% with both indices. *Koanophyllon pittieri* dispersal limitation was similar using presence and density indices; *K. pittieri* seeds were present in 54% of the seed traps, ranging from one to 116 seeds in one seed trap (Figure 1.7.3). The presence index ranked dispersal limitation much lower for *Heliocarpus appendiculatus* (~20%) than density-weighted dispersal limitation (close to 60%, Figure 1.7.3). Even though this common pioneer occurred in 74% of the seed traps, the number of seeds per trap was low overall (mean 3 ± SD 1.3 seeds); the species was well represented in space, but not in numbers in the total seed sample. This is also a species with highly variable seed germination; germination rates may be higher than 60% or as low as 10%, depending on the conditions of the site where the seed falls (mean 35 ± SD15%; Vázquez-Yanes and Orozco-Segovia 1992, Holl 1999).

Establishment limitation in the pasture was comparable for presence and density indices for all species with two exceptions, *Cecropia obtusifolia* and *Bursera simaruba*. The presence index indicated less limitation than the density-weighted index. *C. obtusifolia* was found in 15% of the seed traps, ranging from 1 to 19 seeds. Seeds were most often found in sites with seedlings of the species. In contrast, *B. simaruba* recruits were less limited, based on

the density-weighted index (Figure 1.7.3). *Bursera* seedlings were found in 33% of all the sites, ranging from 1 to 31 seedlings per site. The paradox for this species is that only seven seeds of *B. simaruba* fell into the seed traps and none of them were found in sites where recruits were found.

Over all habitats, the differences between the two indices were higher for later successional than for pioneer species (P < 0.01); the density-weighted index estimated more dispersal limitation for later-successional species. Among later-successional species, establishment limitation was lower using the density-weighted index than the presence index (P < 0.001; Figure 1.7.4). A similar discrepancy between the two indices occurred when comparing animal and wind-dispersed species. Overall dispersal imitation for animal and wind-dispersed species did not vary significantly between indices. On the other hand establishment limitation was estimated lower for animal-dispersed species using the density-weighted index than the limitation shown by wind-dispersed species (P < 0.001, Figure 1.7.4).

1.4 DISCUSSION

Implications of dispersal and recruitment limitation have a long history in plant ecology. For decades, the primary focus was on consequences of long-distance dispersal for plant biogeography, an emphasis that remains relevant in predicting and evaluating colonization of distant habitats (Ridley 1930, MacArthur and Wilson 1967, Clark 1998, Hubbell 2001). Advantages also occur when seeds are dispersed much longer distances from conspecific adults because density-dependent seed or seedling mortality from pathogens, insects, other enemies or competition are greater near fruiting trees (Janzen 1970, Connell 1971, Howe and Smallwood 1982, Clark et al. 1999, Comita et al. 2010) .

Moreover, Harms and colleagues (2000) found a general negative effect of density on seed survival and seedling emergence independent of samples close to fruiting trees. It has since become clear that mortality may be density-dependent or density-independent at different stages of plant development, from seeds to adults (Clark et al. 2013). Our interest is the difference between dispersal and establishment limitation by habitat, a set of contrasts that is rarely studied.

Here we address this community-level perspective by evaluating dispersal and establishment limitation in primary forest, secondary forest and pasture habitats. Habitats differ greatly in the number and species composition of seeds arriving, and likewise differ greatly in the factors that favor recruitment of some species from the seed rain over others. Given differences in genotype and viability among seed and seedling cohorts, chances of success are greater in a space with 10 or 100 genetic "lottery tickets" than for one ticket (*sensu* Williams 1975). The distinction between dispersal limitation and establishment limitation is particularly important in the colonization of open areas no longer subject to agriculture or grazing, where sparse seed rain and low seedling survival limit natural succession and managed restoration (Martínez-Garza and González-Montagut 1999, Boucher et al. 2001, Ingle 2003, Martínez-Garza and Howe 2003, Chazdon et al. 2007, Martínez-Garza et al. 2009, Howe et al. 2010). Our general question is whether dispersal limitation and establishment limitation differ in forest and pasture habitats.

Low seed input in pastures is one of the most important barriers to forest regeneration in tropical landscapes (Slocum 2001). A very low transition probability between seed fall and juvenile recruitment is common (Harms et al. 2000, Norden et al. 2009). Dispersal limitation may be a major factor for most species in species-rich plant communities (Platt

and Weis 1977, Tilman 1994, Hurtt and Pacala 1995). Recruitment limitation is likely to be most pronounced in highly diverse communities because so many species are rare, resulting in lower seed rain for rare species than for abundant species (Hurtt and Pacala 1995, Terborgh et al. 2011, ter Steege et al. 2013). Higher seed densities increase seedling recruitment but may also induce density dependent mechanisms that act on high seedling densities, resulting in population regulation (Clark et al. 2013). Intra- or interspecific competition in these forming communities matters.

Dispersal limitation incorporates quantity of seed rain and dispersion in space. Existing models evaluating dispersal limitation do not address factors such as the densities in which seeds arrive, dispersal strategies, seed size, seed quality or abundance of seeds of other species. We use indices that include a component of density of seeds and seedlings in evaluating limitations to successful dispersal and establishment (density-weighted index). Our results show that limitation patterns are distinctively different between the habitats. The secondary forest is saturated with seeds (45,386 seeds in 1 m^2/year), with 88% from one wind-dispersed pioneer species (*Trichospermum galeotii*) with complete establishment limitation - no seedlings established in the secondary forest). In primary forest, limitation varied among species. A striking case was *N. ambigens*, for which the presence index estimated high establishment limitation and the density-weighted index estimated moderate limitation. This is particularly important because *N. ambigens* represented 89% of the total sample of recruits in primary forest, hardly establishment-limited. In primary forest, dispersal limitation has been suggested as the major factor contributing to the maintenance of plant diversity at scales of community, landscape, region and ecosystem (Tilman 1994, Hurtt and Pacala 1995, Hubbell et al. 1999). On the

other hand, in pastures with zero presence of reproductive conspecific or heterospecific trees, dispersal limitation shapes the initial composition, even if subsequent establishment limitation is high. Almost all species exhibited dispersal limitation in pastures. Only seeds of pioneer tree species dispersed by wind occurred in pastures with any regularity, and of those only three pioneer species were even moderately successful in recruitment (*C. alliodora, H. appendiculatus* and *K. pittieri*). Under a scenario of natural succession, the future composition of abandoned pastures will lead to "pioneer deserts" (sensu Martínez-Garza and Howe 2003).

Wind-dispersed species arrive in open pastures in high densities, but establishment limits them. Wind-dispersed trees with small seeds often disperse better into open degraded areas than animal-dispersed species (Zimmerman et al. 2000, Cubina and Aide 2001, Vieira and Scariot 2006). In abandoned pasturelands adjacent to primary rainforest of southern Costa Rica, the seed rain of animal-dispersed species is dramatically reduced > 5m away from the forest edge (Holl 1999). This higher dispersal capacity should result in an over-representation of wind-dispersed species in tropical pastures (Posada et al. 2000). Nevertheless, even when wind-dispersed species have higher densities of dispersed seeds, they represent a small fraction of the diversity of tropical rainforests (Holl 1999). Our results are consistent with these observations. *Trichospermum galeottii*, *Heliocarpus appendiculatus*, *Koanophyllon pittieri* and *Cordia alliodora* were vastly over-represented in the pasture seed rain, but not in the seedling composition. This suggests that succession towards primary forest composition will be slow and circuitous with respect to species composition and abundance patterns.

Species often differ in the life stage that limits population growth. In the present study, species with lower dispersal limitation are not necessarily the ones with lower establishment limitation. This is consistent with studies in the African Congo in which species with low dispersal limitation show high establishment limitation in primary forests, suggesting a trade-off between dispersal and establishment capacity. Extremely high seed densities are offset by density-dependent mortality of seedlings (Muller-Landau 2010, Clark et al. 2013). Different results are found in Nouragues, French Guinea, where dispersal and establishment limitation are evaluated using the presence index for 14 tree species (Norden et al. 2009). Establishment limitation for dominant species allowed poor competitors to occupy sites (Hurtt and Pacala 1995, Norden et al. 2009). The seeds of species that arrive in the pastures are from a different subset of species than those found in the forest (Martínez-Garza et al. 2009). Notably, in the present study establishment limitation is indistinguishable among the three habitats using the presence index, yet the density-weighted index shows that secondary forest has substantially less limitation than pastures which agree with a successional habitat experiencing high colonization rates. The overall conclusion is that succession in pastures is impeded by both limited seed arrival and by lower capacity of seeds to germinate and seedlings to establish and survive.

1.4.1 Management implications

The distinction between dispersal and establishment limitation potentially leads to better management decisions. When a species is dispersal-limited but has a high establishment probability, management strategies for a given habitat can focus on facilitating the dispersal of the seeds, for example by direct seeding (Turnbull et al. 2000, Camargo et al. 2002). This is less time-consuming, less logistically challenging and less costly than rearing

seedlings. If limitation is not seed availability but establishment availability, different

management strategies are indicated. It is best to germinate seeds and grow seedlings to a

viable size in growing houses, and then plant them at the site at suitable sizes (Martínez-

Garza et al. 2013). Another approach would attract animal dispersers into a pasture by

planting trees that offer cover and food resources in fruit crops (de la Peña-Domene et al.

2014). In the latter case tree species arriving cannot be controlled, but the method can

become self-reinforcing as animal-dispersed species arrive and mature.

1.5 LITERATURE CITED

Arroyo-Rodríguez, V., J. C. Dunn, J. Benítez-Malvido, and S. Mandujano. 2009. Angiosperms, Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. Check List, Campinas 5:787-799.

Boucher, D. H., J. H. Vandermeer, I. Granzow de la Cerda, M. A. Mallona, I. Perfecto, and N. Zamora. 2001. Post-agriculture versus post-hurricane succession in southeastern Nicaraguan rain forest. Plant Ecology 156:131-137.

Boyle, B., N. Hopkins, Z. Lu, J. A. Raygoza Garay, D. Mozzherin, T. Rees, N. Matasci, M. Narro, W. Piel, S. Mckay, S. Lowry, C. Freeland, R. Peet, and B. Enquist. 2013. The taxonomic name resolution service: an online tool for automated standardization of plant names. BMC Bioinformatics 14:16.

Brokaw, N. V. L., and S. M. Scheiner. 1989. Species composition in gaps and structure of a tropical forest. Ecology 70:538-541.

Buschbacher, R. J. 1986. Tropical deforestation and pasture development. Bioscience 36:22-28.

Camargo, J. L. C., I. D. K. Ferraz, and A. M. Imakawa. 2002. Rehabilitation of Degraded Areas of Central Amazonia Using Direct Sowing of Forest Tree Seeds. Restoration Ecology 10:636-644.

Clark, C. J., J. R. Poulsen, and D. J. Levey. 2013. Roles of Seed and Establishment Limitation in Determining Patterns of Afrotropical Tree Recruitment. Plos One 8:e63330.

Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. American Naturalist 152:204-224.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed Dispersal near and Far: Patterns across Temperate and Tropical Forests. Ecology 80:1475-1494.

Colwell, R. K. 2006. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.0 User's Guide and application. published at: http://viceroy.eeb.uconn.edu/estimates.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science 329:330-332.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Cubina, A., and T. M. Aide. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. Biotropica 33:260-267.

Chazdon, R. L., S. G. Letcher, M. van Breugel, M. Martinez-Ramos, F. Bongers, and B. Finegan. 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philosophical Transactions of the Royal Society B-Biological Sciences 362:273-289.

de la Peña-Domene, M., C. Martínez-Garza, and H. F. Howe. 2013. Early recruitment dynamics in tropical restoration. Ecological Applications 23:1124-1134.

Engelbrecht, B. M. J., S. J. Wright, and D. De Steven. 2002. Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. Journal of Tropical Ecology 18:569-579.

Estrada, A., and R. Coates-Estrada. 2001. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. Pages 627-646. Cambridge Journals Online.

Estrada, A., and R. Coates-Estrada. 2005. Diversity of Neotropical migratory landbird species assemblages in forest fragments and man-made vegetation in Los Tuxtlas, Mexico. Biodiversity and Conservation 14:1719-1734 (1716).

Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in amazonian forests. Science 305:663-665.

García-Orth, X., and M. Martínez-Ramos. 2008. Seed dynamics of early and late successional tree species in tropical abandoned pastures: seed burial as a way of evading predation. Restoration Ecology 16:435-443.

González Soriano, E., R. Dirzo, and R. C. Vogt. 1997. Historia natural de los Tuxtlas. 1. edition. Universidad Nacional Autónoma de México Instituto de Ecología, México.

Guevara, S., and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio 107/108:319-338.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493-495.

Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31:229-242.

Holl, K. D., E. E. Crone, and C. B. Schultz. 2003. Landscape restoration: moving from generalities to methodologies. Bioscience 53:491-502.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Howe, H. F., Y. Urincho-Pantaleon, M. de la Peña-Domene, and C. Martinez-Garza. 2010. Early seed fall and seedling emergence: precursors to tropical restoration. Oecologia 164:731-740.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. de Lao. 1999. Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. Science 283:554-557.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation - reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176:1-12.

Ingle, N. R. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. Oecologia 134:251-261.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501-527.

Jones, F. A., C. J. Peterson, and B. L. Haines. 2003. Seed predation in neotropical pre-montane pastures: site, distance, and species effects. Biotropica 35:219-225.

Kitajima, K. 2002. Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. Functional Ecology 16:433-444.

Laborde, J., S. Guevara, and G. Sanchez-Rios. 2008. Tree and shrub seed dispersal in pastures: The importance of rainforest trees outside forest fragments. EcoScience 15:6-16.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton. N. J. .

Martinez-Garza, C., F. Bongers, and L. Poorter. 2013. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? Forest Ecology and Management 303:35-45.

Martínez-Garza, C., A. Flores-Palacios, M. De La Peña-Domene, and H. F. Howe. 2009. Seed rain in a tropical agricultural landscape. Journal of Tropical Ecology 25:541-550.

Martínez-Garza, C., and R. González-Montagut. 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecology 145:255-265.

Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. Journal of Applied Ecology 40:423-429.

Martínez-Garza, C., W. Tobon, J. Campo, and H. F. Howe. 2013. Drought mortality of tree seedlings in an eroded tropical pasture. Land Degradation & Development:287-295.

Muller-Landau, H. C. 2010. The tolerance–fecundity trade-off and the maintenance of diversity in seed size. Proceedings of the National Academy of Sciences 107:4242-4247.

Muller-Landau, H. C., S. J. Wright, O. Calderón, S. P. Hubbell, and R. B. Foster. 2002. Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. Pages 35-53 *in* D. J. Levey, W. R. Silva, and M. Galetti, editors. Seed Dispersal and Frugivory. CAB International, Wallingford.

Myster, R. W. 2003. Vegetation dynamics of a permanent pasture plot in Puerto Rico. Biotropica 35:422-428.

Myster, R. W. 2004. Post-agricultural invasion, establishment, and growth of neotropical trees. Botanical Review 70:381-402.

Nathan, R., F. M. Schurr, O. Spiegel, O. Steinitz, A. Trakhtenbrot, and A. Tsoar. 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology & Evolution 23:638-647.

Nepstad, D., C. Uhl, and A. E. Serrão. 1990. Surmounting barriers to forest regeneration in abandoned highly degraded pastures: a case study from Paragominas, Pará, Brazil. Pages 215-229 *in* A. B. Anderson, editor. Alternatives to deforestation: steps toward sustainable use of the amazon rain forest. Columbia University Press, New York, N.Y.

Nepstad, D. C., C. Uhl, and E. A. S. Serrao. 1991. Recuperation of a Degraded Amazonian Landscape - Forest Recovery and Agricultural Restoration. Ambio 20:248-255.

Norden, N., J. Chave, P. Belbenoit, A. Caubere, P. Chatelet, P. M. Forget, B. Riera, J. Viers, and C. Thebaud. 2009. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. Journal of Ecology 97:186-197.

Palmiotto, P. A., S. J. Davies, K. A. Vogt, M. S. Ashton, D. J. Vogt, and P. S. Ashton. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. Journal of Ecology 92:609-623.

Parrotta, J. A. 1995. Influence of Overstory Composition on Understory Colonization by Native Species in Plantations on a Degraded Tropical Site. Journal of Vegetation Science 6:627-636.

Platt, W. J., and I. M. Weis. 1977. Resource Partitioning and Competition within a Guild of Fugitive Prairie Plants. The American Naturalist 111:479-513.

Posada, J. M., T. M. Aide, and J. Cavelier. 2000. Cattle and Weedy Shrubs as Restoration Tools of Tropical Montane Rainforest. Restoration Ecology 8:370-379.

Reid, J. L., and K. D. Holl. 2013. Arrival ≠ Survival. Restoration Ecology 21:153-155.

Rhoades, C. C., G. E. Eckert, and D. C. Coleman. 1998. Effect of Pasture Trees on Soil Nitrogen and Organic Matter: Implications for Tropical Montane Forest Restoration. Pages 262-270.

Ridley, H. N. 1930. The Dispersal of Plants Throughout the World. Reeve, Ashford, UK.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology 82:2547-2559.

Sork, V. L. 1987. Effects of predation and light on seedling establishment in *Gustavia superba*. Ecology 68:1341-1350.

ter Steege, H., N. C. A. Pitman, D. Sabatier, C. Baraloto, R. P. Salomão, J. E. Guevara, O. L. Phillips, C. V. Castilho, W. E. Magnusson, J.-F. Molino, A. Monteagudo, P. Núñez Vargas, J. C. Montero, T. R. Feldpausch, E. N. H. Coronado, T. J. Killeen, B. Mostacedo, R. Vasquez, R. L. Assis, J. Terborgh, F. Wittmann, A. Andrade, W. F. Laurance, S. G. W. Laurance, B. S. Marimon, B.-H. Marimon, I. C. Guimarães Vieira, I. L. Amaral, R. Brienen, H. Castellanos, D. Cárdenas López, J. F. Duivenvoorden, H. F. Mogollón, F. D. d. A. Matos, N. Dávila, R. García-Villacorta, P. R. Stevenson Diaz, F. Costa, T. Emilio, C. Levis, J. Schietti, P. Souza, A. Alonso, F. Dallmeier, A. J. D. Montoya, M. T. Fernandez Piedade, A. Araujo-Murakami, L. Arroyo, R. Gribel, P. V. A. Fine, C. A. Peres, M. Toledo, G. A. Aymard C., T. R. Baker, C. Cerón, J. Engel, T. W. Henkel, P. Maas, P. Petronelli, J. Stropp, C. E. Zartman, D. Daly, D. Neill, M. Silveira, M. R. Paredes, J. Chave, D. d. A. Lima Filho, P. M. Jørgensen, A. Fuentes, J. Schöngart, F. Cornejo Valverde, A. Di Fiore, E. M. Jimenez, M. C. Peñuela Mora, J. F. Phillips, G. Rivas, T. R. van Andel, P. von Hildebrand, B. Hoffman, E. L. Zent, Y. Malhi, A. Prieto, A. Rudas, A. R. Ruschell, N. Silva, V. Vos, S. Zent, A. A. Oliveira, A. C. Schutz, T. Gonzales, M. Trindade Nascimento, H. Ramirez-Angulo, R. Sierra, M. Tirado, M. N. Umaña Medina, G. van der Heijden, C. I. A. Vela, E. Vilanova Torre, C. Vriesendorp, O. Wang, K. R. Young, C. Baider, H. Balslev, C. Ferreira, I. Mesones, A. Torres-Lezama, L. E. Urrego Giraldo, R. Zagt, M. N. Alexiades, L. Hernandez, I. Huamantupa-Chuquimaco, W. Milliken, W. Palacios Cuenca, D. Pauletto, E. Valderrama Sandoval, L. Valenzuela Gamarra, K. G. Dexter, K. Feeley, G. Lopez-Gonzalez, and M. R. Silman. 2013. Hyperdominance in the Amazonian tree flora. Science 342.

Terborgh, J., P. Alvarez-Loayza, K. Dexter, F. Cornejo, and C. Carrasco. 2011. Decomposing dispersal limitation: limits on fecundity or seed distribution? Journal of Ecology 99:935-944.

Tilman, D. 1994. Competition and Biodiversity in Spatially Structured Habitats. Ecology 75:2-16.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225-238.

Turner, I. M. 2001. The Ecology of Trees in the Tropical Rain Forest. Cambridge University Press.

Vázquez-Yanes, C., and A. Orozco-Segovia. 1992. Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. Tree Physiology 11:391-400.

Vieira, D. L. M., and A. Scariot. 2006. Principles of natural regeneration of tropical dry forests for restoration. Restoration Ecology 14:11-20.

Wijdeven, S. M. J., and M. E. Kuzee. 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. Restoration Ecology 8:414-424.

Williams, G. C. 1975. Sex and evolution. Princeton University Press, N. J.

Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology 8:350-36

1.6 TABLES

Table 1.6.1. Seed mass (g), seeds and recruit abundances and life history and dispersal mode categories by habitat, where s_i is total seeds collected of species i in traps in a habitat, and r_i is total recruits of species i in adjacent habitat.

Species	Family	Seed mass	S_i	R_i	Life history[1]	Dispersal mode
Primary forest						
Astrocaryum mexicanum Liebm. ex Mart.	ARECACEAE	3.4220	3	3	Late	Animal
Chamaedorea tepejilote Liebm.	ARECACEAE	0.1750	26	7	Late	Animal
Cordia alliodora (Ruiz & Pav.) Oken	BORAGINACEAE	0.0330	1	1	Pioneer	Wind
Cupania glabra Sw.	SAPINDACEAE	0.1900	30	4	Late	Animal
Cymbopetalum baillonii R.E. Fr.	ANNONACEAE	0.3335	1	4	Late	Animal
Faramea occidentalis (L.) A. Rich.	RUBIACEAE	0.3000	5	6	Late	Animal
Nectandra ambigens (S.F. Blake) C.K. Allen	LAURACEAE	1.8000	13	20	Late	Animal
Piper amalago L.	PIPERACEAE	0.0015	2	3	Pioneer	Animal
Notopleura chapensis (Steyerm.) C.M. Taylor	RUBIACEAE	0.2100	7	3	Late	Animal
Stemmadenia donnell-smithii (Rose) Woodson	APOCYNACEAE	0.0700	7	1	Pioneer	Animal
Trichilia martiana C. DC.	MELIACEAE	0.2364	1	26	Late	Animal
Virola guatemalensis (Hemsl.) Warb.	MYRISTICACEAE	0.1962	73	10	Late	Animal
TOTAL			169	78		
Secondary forest						
Astrocaryum mexicanum Liebm. ex Mart.	ARECACEAE	3.4220	2	5	Late	Animal
Bursera simaruba (L.) Sarg.	BURSERACEAE	0.1170	148	1	Late	Animal
Carica papaya L.	CARICACEAE	0.0230	9	14	Pioneer	Animal
Chamaedorea alternans H. Wendl.	ARECACEAE	0.1750	5	2	Late	Animal
Cnidoscolus multilobus (Pax) I.M. Johnst.	EUPHORBIACEAE	0.0800	18	6	Late	Animal
Cojoba arborea (L.) Britton & Rose	FABACEAE	0.8500	36	2	Pioneer	Wind
Cupania glabra Sw.	SAPINDACEAE	0.1900	236	2	Late	Animal
Eugenia capuli (Schltdl. & Cham.) Hook. & Arn.	MYRTACEAE	0.0560	1	3	Late	Animal
Hampea nutricia Fryxell	MALVACEAE	0.1100	3	2	Pioneer	Wind
Heliocarpus appendiculatus Turcz.	MALVACEAE	0.0015	4,574	9	Pioneer	Wind

Piper amalago L.	PIPERACEAE	0.0015	13	8	Pioneer	Animal
Psychotria veracruzensis Lorence & Dwyer	RUBIACEAE	0.0020	9	2	Late	Animal
Rollinia jimenezii Saff.	ANNONACEAE	0.1600	5	1	Late	Animal
Trichospermum galeottii (Turcz.) Kosterm.	MALVACEAE	0.0030	40,319	5	Pioneer	Wind
Vachellia cornigera (L.) Seigler & Ebinger	FABACEAE	0.0760	8	3	Pioneer	Wind
TOTAL			45,386	62		
Pastures						
Bursera simaruba (L.) Sarg.	BURSERACEAE	0.1170	7	104	Late	Animal
Cecropia obtusifolia Bertol.	URTICACEAE	0.0010	31	28	Pioneer	Animal
Conostegia xalapensis (Bonpl.) D. Don ex DC.	MELASTOMATACEAE	0.0001	184	23	Pioneer	Animal
Cordia alliodora (Ruiz & Pav.) Oken	BORAGINACEAE	0.0330	457	54	Pioneer	Wind
Cupania glabra Sw.	SAPINDACEAE	0.1900	12	3	Late	Animal
Heliocarpus appendiculatus Turcz.	MALVACEAE	0.0015	167	20	Pioneer	Wind
Heliocarpus donnellsmithii Rose	MALVACEAE	0.0010	1	4	Pioneer	Wind
Koanophyllon pittieri (Klatt) R.M. King & H. Robinson	ASTERACEAE	0.0009	376	2	Pioneer	Wind
Ochroma pyramidale (Cav. ex Lam.) Urb.	MALVACEAE	0.0080	1	1	Pioneer	Wind
Piper amalago L.	PIPERACEAE	0.0015	5	5	Pioneer	Animal
Stemmadenia donnell-smithii (Rose) Woodson	APOCYNACEAE	0.0700	2	1	Pioneer	Animal
Tetrorchidium rotundatum Standl.	EUPHORBIACEAE	0.0480	7	24	Late	Animal
Trema micrantha (L.) Blume	CANNABACEAE	0.0070	1	5	Pioneer	Animal
TOTAL			1,251	304		

1.7 FIGURES
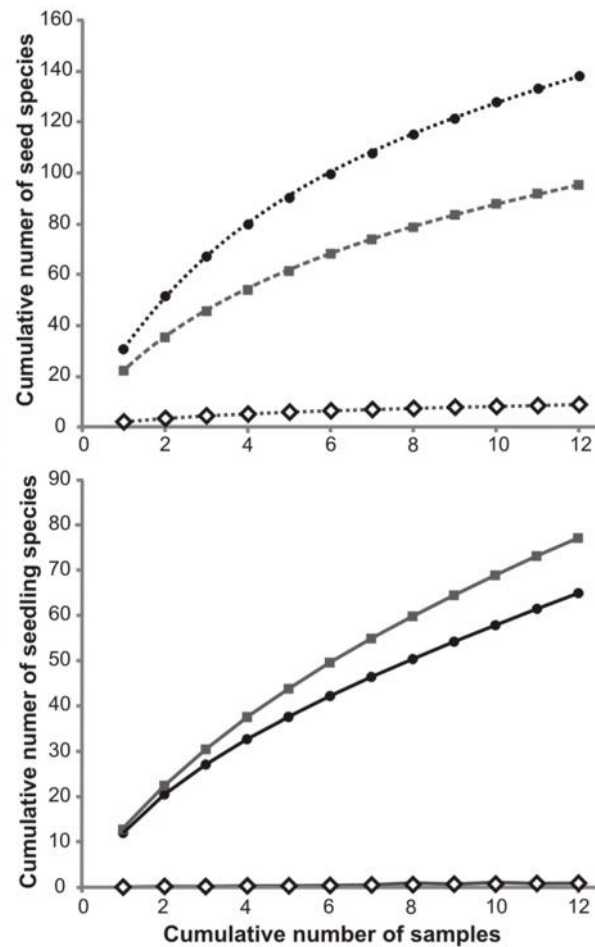
Figure 1.7.1. Species accumulation (Mao Tau) of seed and recruit samples up to 24 months after planting. Each sample is a species count in 1-m2 seed trap (for seeds) and 5 adjacent m2 (for seedlings), with 12 samples of each per habitat per census. Black circles represent the primary forest (seed species at the top and seedling species at the bottom), gray squares are the secondary forests and the open diamonds are the pasture lands. Dashed lines are for seed rain and continuous lines are for seedlings. For the purpose of metrics (Table 1), the sample area for pasture is increased as indicated in the text.
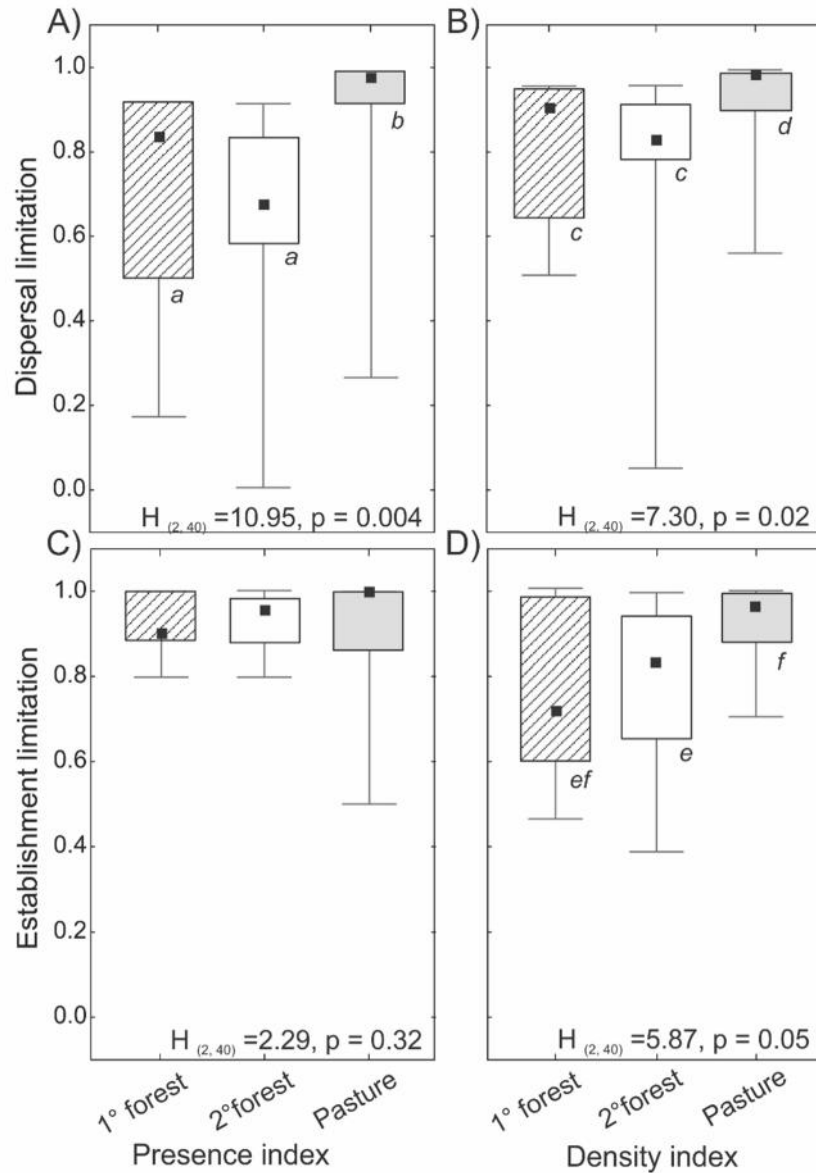
Figure 1.7.2. Comparison of presence and density indices for primary forest, secondary forest, and fenced pasture at Los Tuxtlas, southern Mexico. Presence and density-weighted indices are shown for dispersal limitation (A and B, respectively), and for establishment limitation (C and D, respectively). Squares show medians, boxes are quartiles and bars indicate highest and lowest values. Different letters indicate significance based on multiple comparison z-tests within each frame. See text for relevant comparisons between frames.
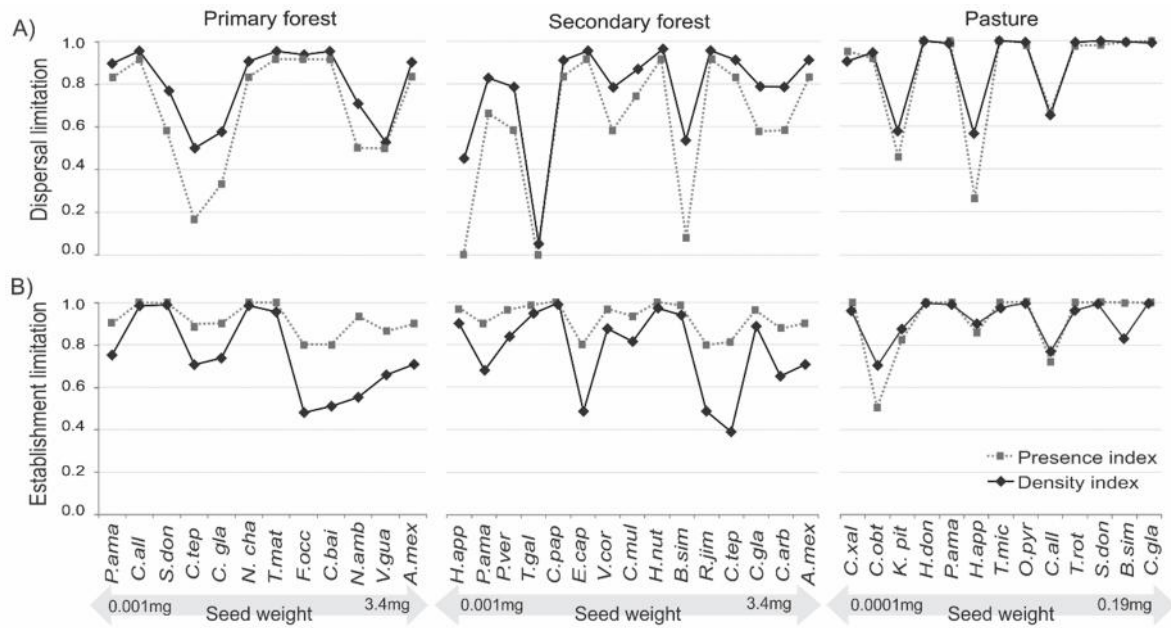
Figure 1.7.3. Graphic representation of the differences between the presence and the density-weighted index. The connecting line is only to show how a general tendency is followed for both indexes. Wald-Wolfowitz Runs Test indicated highly significant differences for both A) dispersal and B) establishment limitation between indices (Z_{adj}=4.16, P = 0.00003 and Z_{adj}=3.71, P = 0.0002, respectively).
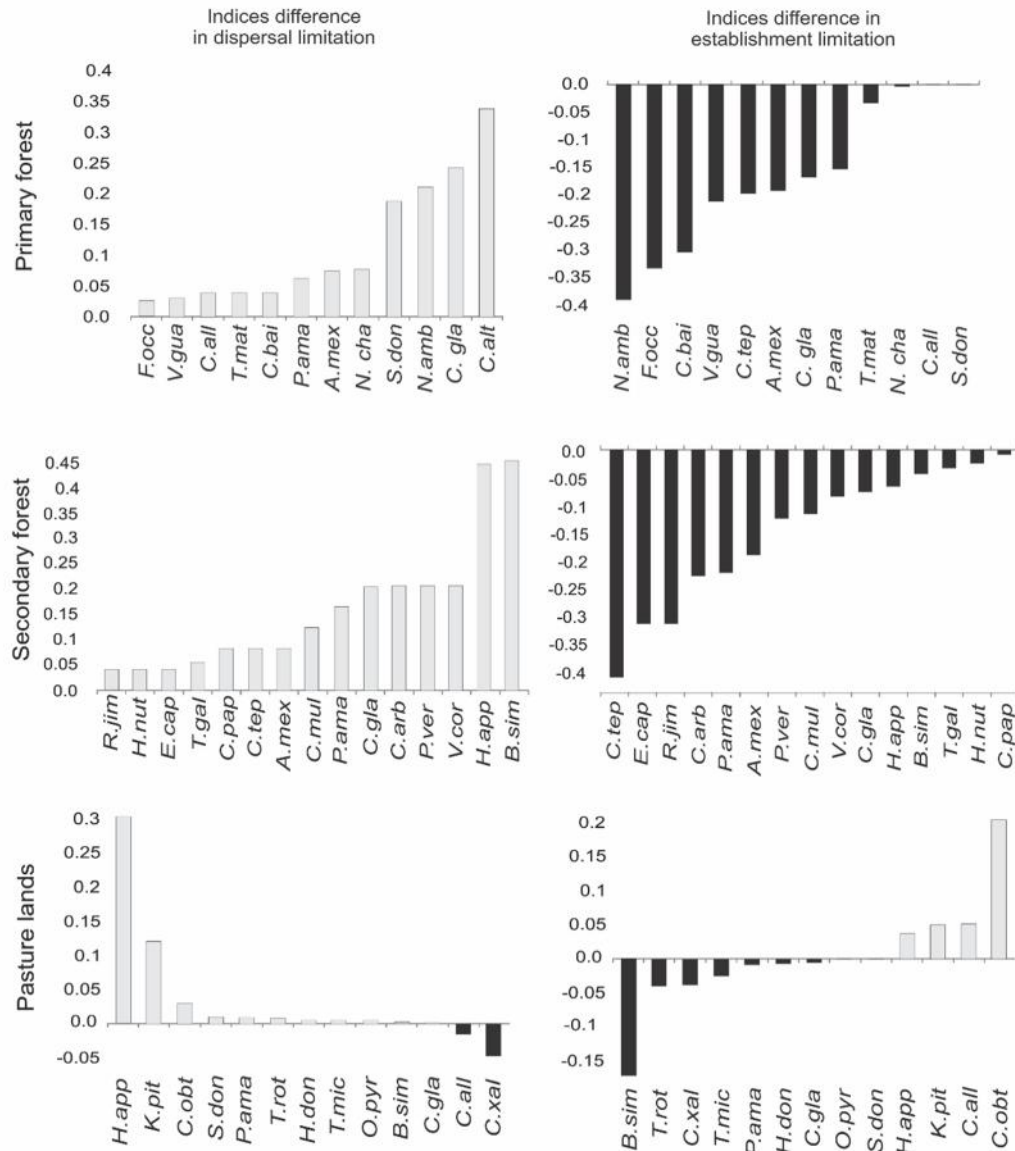
Figure 1.7.4. Differences between the presence and the density-weighted index in three different habitats, using differences between presence and density-weighted indices for recruiting species. Positive values indicate that the density-weighted index showed higher limitation than the presence index. Negative values indicate that less limitation was estimated by the density-weighted index. Species are ordered based on the size of the difference between indices.

Chapter II

2. TROPICAL SEED POTENTIAL OR REALIZED EFFECTIVENESS?

Tropical seed potential or realized effectiveness?

Marinés de la Peña-Domene, Henry F. Howe, Emiliano Cruz-León, Yuliana Urincho-Pantaleón, Rita Jiménez-Rolland, Cesar Lozano-Huerta, and Cristina Martínez-Garza

2.1 INTRODUCTION

Darwin (p. 62) commented that "a plant on the edge of a desert is said to struggle for life against the drought." The fact that not all species struggle to the same degree against drought, shade, competing plants, disease or insects is central to understanding recruitment dynamics in primary forests, and is of particular importance in understanding natural or assisted succession of abandoned agricultural land back to forest (Rudel *et al.* 2005; Chazdon 2008). A compelling current question is the degree to which seed fall provides predictable templates of later community structure (Schupp *et al.* 1989; Clark 1998; Hubbell 2001), or reflects unrealized potential due to recruitment limitation in time and space (Hubbell *et al.* 1999; Schupp, Jordano & Gomez 2010; Swamy *et al.* 2011). Here we offer quantitative prognoses of regeneration from seeds of rainforest trees using "seed effectiveness (Table 2.8.1)". This is an estimate of seed success in producing an established juvenile that integrates the number of seeds of a species it takes to produce a recruit, the seeds germinating per unit area, and the relative contribution of a species compared with others for recruitment at a given time in a given habitat. The point is to offer a community-level insight into the consequences of seed dispersal and ensuing processes, as well as insight into characteristics of species that both arrive and survive under different circumstances.

Limitations of seed arrival and survival are instructive. In mature rainforest of Barro Colorado Island, arrival of seeds of a given species is sparse more than a few meters from fruiting trees (Harms *et al.* 2000; Wright *et al.* 2005). Seed addition experiments show that natural seed fall produces much less seedling recruitment than is possible for 31 of 32 species tested in continuous forest rich in bird and mammalian dispersal agents (Svenning & Wright 2005). In the same forest, pervasive density-dependent mortality of woody vine and tree seeds indicates that seed potential is limited under circumstances where mortality from pathogens and insects have high encounter frequency with seeds (Harms *et al.* 2000). Coupled with density-independent mortality of seeds and seedlings from drought, physiological stress, and a variety of other often unknown causes (e.g. Harper 1977; Howe 1990; see Moles & Westoby 2004), there is every reason to expect a clear disparity between seed potential and realized effectiveness.

Seed size and dispersal mode can also be expected to influence realization of seed potential. In general, small seed size is advantageous for pioneer species that disperse widely to open, sparsely-vegetated habitats, while larger seeds confer an advantage to seedlings that establish in shade (Harms & Dalling 1997; Dalling, Hubbell & Silvera 1998; Kitajima 2002). Within forests, species that allocate resources to many small seeds produce greater seed rain per unit area, while species that allocate resources to a smaller number of larger seeds produce a sparser seed rain with a better chance of survival in shaded understory (Moles *et al.* 2004). While there are ample *á priori* reasons to expect general seed and establishment limitation in tropical forest understory, an open question is how realized seed potential can be estimated and communicated across species, life-histories, dispersal modes, and habitats.

Disparities of tree-seed arrival and survival are exaggerated on recently abandoned agricultural land. Seed fall in pastures is sparse and strongly biased towards small seeds of pioneer species (Uhl 1987; Nepstad *et al.* 1996; Martínez-Garza & González-Montagut 1999; Ingle 2003; Martínez-Garza *et al.* 2009). Once arrived, survival of seeds and small seedlings is often compromised by dry-season drought so severe that a desert metaphor is plausible (Martínez-Garza *et al.* 2011b), and by thick grasses that suppress either germination or early seedling growth (Aide *et al.* 1995). An ecological paradox is that the vast majority of seeds of species that arrive in extensive pastures are small, yet conditions favor survival of taxa with larger seeds that produce larger seedlings (Holl 1999; Zimmerman, Pascarella & Aide 2000; Poorter *et al.* 2008). Species with dispersal-limited large seeds often survive well in early-successional habitats if they manage to get there (Martinez-Garza *et al.* 2005). While seed dispersal is limiting in all habitats, dispersal limitation and recruit mortality are extreme filters to regeneration on recently abandoned agricultural land.

We build upon recent interest in seed and establishment limitation to explore metrics that permit assessments across communities for guilds and species of tropical plants. Key insights from earlier work are that many places do not receive as many seeds of a given species as they potentially could, and that many seeds that arrive fail to make the transition to seedlings or from seedlings to older juveniles (Muller-Landau *et al.* 2002; Clark *et al.* 2007; Norden *et al.* 2009a; Terborgh *et al.* 2011). Extending this approach, we ask how many seeds of a given species it takes to produce a recruit per unit area in primary forest, secondary forest, or recently abandoned pasture. This calculation allows us to further ask whether seed effectiveness and relative effectiveness differ by life-history guilds or dispersal modes.

Here we ask whether metrics developed to estimate seed potential vary by ecological circumstance (definitions in Table 2.8.1). In particular, we ask whether the number of seeds required to produce a seedling (Φ_i), effective seeds arriving at a station (E_{it}), and relative seed effectiveness among all effective seeds arriving at a station (ε_{it}) differ in primary and secondary forest and recently-fenced pasture, partitioned by life-history and dispersal mode. In each analysis, we hypothesize that Φ_i will be greater in pasture than forest, and further that E_{it}, and ε_{it} will be greater in primary than secondary forest, and in either forest habitat than pasture. Expected differences would be consistent with expectations of seed size, which in turn reflects pioneer and later-successional life histories, and animal- and wind-mediated dispersal modes. Contrary results would indicate rough parity of realized seed potential in different habitats. All metrics are of widely-dispersed seeds and seedlings, not seedling cohorts near parent trees. This is an early contribution of an experiment expected to last 30 years, and the first to evaluate quantitative metrics of seed effectiveness by habitat, life-history status, and dispersal mode.

2.2 METHODS

2.2.1 Study Site and Sampling

The Los Tuxtlas Biological Station (LTBS) lies within a reserve of 640 ha of lowland tropical rain forest, continuous with 3500 additional ha, in the state of Veracruz, southeast Mexico (description and botanical check-list in González Soriano, Dirzo & Vogt 1997). The forest has a closed canopy ~ 35 m high. The most common species in the forest canopy is *Nectandra ambigens*; while in the mid-canopy, *Pseudolmedia oxyphyllaria* is most the abundant and *Astrocaryum mexicanum* in the understory (Bongers *et al.* 1988). Mean annual

temperature and rainfall are 27º C and 4900 mm, respectively.   Normal dry season extends from March to May, rainy season from June to February.

The site is a cow pasture that has been intensively grazed for 30-40 years, embedded in a mosaic pasture, isolated trees or stands of trees, and primary and secondary forest. Twenty-four fenced 30 x 30 m plots separated by 35 m of grazed pasture are arranged in a 3 x 8 grid (central GPS point 18º 35′ 43.64″ N, 95º 06′ 06.29″ W) adjacent to the LTBS (nearest GPS point 18º 35′ 18.7″ N, 95º 06′ 25.7″ W) facing NE to the Gulf of Mexico. Where cattle have access, pasture grasses are a closely cropped 3-10 cm high mix of exotic (*Cynodon plectostachyus*, *C. dactylon*, *Brachiaria decumbens* and *B. brizantha*) and native (*Axonopus compressus, Panicum* spp., *Paspalum conjugatum*) grasses, with *C. plectostachys* originally covering ~ 88% of the ground up to 90 cm deep. Soil is sandy loam classified as vitric andosol originating from basalt and andesite mixed with volcanic ash; soil is acidic (pH 4.9) with a clay (48.5 %) texture (González Soriano, Dirzo & Vogt 1997).

The grid of 24 plots was fenced in pasture of the agricultural Colony of Ruiz Cortínez in July - August 2006. Plots are within 500 to 1200 m of the edge of the LTBS, with the SW corner 90 m from privately owned secondary forest. Individually tagged seedlings of 24 tropical tree species from 15 families were planted in plots from September 2006 to February 2007, and re-planted from August to November 2007 as needed. Eight plots were planted with seedlings of animal-dispersed species, eight with seedlings of wind-dispersed species, and eight left as fenced, unplanted controls. Plantings are not relevant to seed rain here because seedlings were generally 0.2-1 m (0.33 ± 0.2 m) tall by the end of the seed-rain sample. No planted or recruited trees or shrubs reproduced by June 2008.

Seed samples were collected from pasture and forest habitats. Each seed trap consisted of four 1-m poles of PVC supporting 1-m^2 frame covered by a shade cloth net with a rock in the middle to prevent seed roll. Four seed traps in each pasture plot were located at random, stratified by plot quarter, for a total of 96 seed traps, over 14,414 m^2 of recently-fenced pasture. Twelve seed traps in each forest habitat (primary and secondary within continuous forest) ca. 200 m from the forest edge were located at random in an area corresponding to three plots (90 × 30 m). From January 2007 through February 2008, seed samples were collected monthly in pasture and twice a month in forest to avoid early germination, separated, counted and identified to species at the University of the State of Morelos (UAEM), Mexico. Seed identification was done using the herbarium at LTBS and reference collections from previous studies (Martínez-Garza *et al.* 2009). A sample of seeds of each species was preserved and photographed as a reference collection at UAEM. Species were classified as pioneer or later-successional and dispersed by wind or animals with the help of the literature (Martínez-Ramos 1985; Popma, Bongers & Werger 1992; Ibarra-Manriquez & Sinaca 1995; Ibarra-Manriquez & Sinaca 1996a; Ibarra-Manriquez & Sinaca 1996b). Martínez -Garza *et al*. (2009) and Howe *et al*. (2010) provide more detail.

Recruits were censused every four months from June 2007 to June 2008 in pasture, primary forest and secondary forest. Forest recruit samples were from 5 m^2 next to each of 12 seed traps (i.e. 12 stations) in primary and 12 seed traps (12 stations) in secondary forest. The same recruitment area of 5 m^2 close to the traps in pasture yielded virtually no recruits, precluding analysis   Accordingly, we increased seed traps used for calculation of metrics from 12 to 96 in pasture, with four traps per plot, stratified as one in each of four subplots. For each 30 x 30 m plot, this sampled seeds falling in four 13 x 13 m subplots excluding

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space used for bat net lanes, seed traps, and 1 m in from the fences that cows could reach

for a total sample area in pasture of 16,224 m². We report individuals and species recruited

up to 40 mm basal diameter; growth will be explored elsewhere.

While 96 traps are in place in pasture for ongoing studies of succession in planting

treatments, it would be ideal to sample pasture with the same number of sample units

(seed trap for seeds plus 5 m² of understory next to traps for seedlings). As a preliminary

test we employ EstimateS S (Mao Tau: http://viceroy.eeb.uconn.edu/EstimateS; Colwell

2006) to evaluate species accumulation for seeds and seedlings using 12 traps and adjacent

understory for each habitat.

A factor with potential to influence the above measures is seed mass. Seed mass data for

species are taken from species descriptions published in the Royal Botanic Garden

database (http://data.kew.org/sid/sidsearch.html) at Kew Gardens.

Some seed fall and recruitment data overlap with Martínez-Garza *et al*. (2009) and Howe *et*

al. (2010). Martínez-Garza and colleagues evaluate seed rain with respect to habitat; Howe

and colleagues evaluate pasture seed rain and seedling recruitment with respect to spatial

and legacy factors, including proximities of forest edge, living pasture trees, stumps of

trees cut during site preparation, and living fences, as well as soil depth.

2.2.2 Calculations and Analysis

Values and distributions of Φ_i, E_{it} and ε_{it} (Table 2.8.1) are expected to differ among

habitats, species, dispersal modes, and life history profiles. Distributions of Φ_i, E_{it}, and ε_{it}

are highly skewed and not amenable to useful transformation, precluding presentation or

analysis with parametric tools. For ease of visual inspection, we illustrate frequency

distributions or box plots displaying medians and quartiles. Where practical, $\log_{10}$

transformations are used for parametric analyses (e.g. seed mass). Otherwise the basic

tool for analysis is the Kruskal-Wallis test of ranks. Pairwise comparisons employ the

Dwass-Steele-Chritchlow-Fligner test of ranks. Analyses employ Statistica and Systat 13.

2.3 RESULTS

2.3.1 Species accumulation

Extreme differences in density of seeds and seedlings indicate require samples over a

larger area in pasture than in forest. Species accumulation using 12 seed-trap stations

(trap area and 5 m² adjacent understory) in primary and secondary forest show monotonic

increases for seedlings, while stations using the 5 m² areas in pasture show virtually no

increases in seed fall and no recruits at all (Figure 2.7.1). Calculation of community

metrics in pasture using 5 m² seedling sample area per station are uninformative. Use of

all areas of fenced plots in pasture allow calculations for sparse seed fall and much sparser

seedling emergence.

2.3.2 Seed mass

Seed masses of species with records of both seed fall and recruitment differ by four orders

of magnitude, ranging from 0.0001 g seeds in *Constegia xalapensis* berries in pasture to

3.422 g seeds of *Astrocarym mexicanum* in forest. In general, mean seed mass of species

recorded in primary forest (0.578 $\pm$ 0.269 SE g throughout), secondary forest (0.459 $\pm$ 0.245

g), and pasture (0.037 $\pm$ 0.016 g) differed (log transformed data, $F_{2,38}$ = 7.74, P = 0.0015).

Post-hoc Tukey tests indicate that mean seed masses are larger in primary and secondary

forests than pasture (P = 0.0015 and P = 0.032, respectively), while mean seed mass does

not differ between primary and secondary forest (P > 0.3). Mean seed mass is smaller in

pioneer (0.018 ± 0.007 g) than later-successional (0.607 ± 0.202 g) species (with log-transformed data, $F_{1,39}$ = 52.69, P < 0.00001), and less in wind (0.010 ± 0.005 g) than animal-dispersed (0.448 ± 0.153 g) species (log-transformed data, $F_{1,39}$ = 10.04, P = 0.003).

2.3.3 Seeds per recruit Φi

Overall, seeds per recruit ($Φ_i$) decreases with increase in seed mass for the sample of 41 species for which data are available (Figure 2.9.1; r = - 0.55, P < 0.001). Smaller samples by habitat suggest similar negative associations, but only in primary forest does the negative correlation approach significance (r = - 0.50, P = 0.08 for 13 species).

Rankings of seeds per recruit $Φ_i$ differ in primary and secondary forest and in experimentally fenced pasture, which simulate recent abandonment (Figure 2.9.2). Rank distributions of $Φ_i$ differ across habitats (Kruskal-Wallis test of ranks $H_{2, 43}$ = 14.35, P < 0.001). In pairwise tests, pasture and secondary forest are comparable in seeds per recruit (P > 0.70), while primary forest differs from pasture and secondary forest (P = 0.00006 and P < 0.00001, respectively). Seeds per recruit differ widely by species and habitat, with a few species showing extreme values in forest; more in pasture (see Table 2.9.1). Substantial differences between rank order of species are obvious in primary forest (Figure 2.9.2a), where more than 50% of seeds that produce recruits are of the common canopy lauraceous tree *Nectandra ambigens* and understory palm *Chameadora tepejilote*. Estimates of seeds required to produce a recruit are higher in secondary forest, with extremes for pioneer wind-dispersed *Heliocarpus appendiculatus* and *Trichospermum galeotii* of 11,000 and 202,000 seeds per juvenile, respectively (Figure 2.9.2b). Pasture recruits include a few successful colonizers and many poor ones following release from grazing (Figure 2.9.2c). Six species (*Eupatorium galeottii, Hampea nutricia*, *Heliocarpus appendiculatus*, *H. donnell-*

smithii, Ochroma pyramidale and *Trema micrantha*) require > 800 to 7,700 seeds to produce a juvenile in pasture (Table 2.9.1).

Important differences are evident in dispersed seeds per recruit as a function of life history (Figure 1.6.2a, Table 2.8.1). Both seed fall and recruitment are recorded for 19 pioneer and 24 later-successional tree species. Median Φ_i for pioneers (138) is more than an order of magnitude greater than that for later-successional species (10; Mann-Whitney U-test on ranks P = 0.002). Pioneer trees have comparable Φ_i values in the three habitats. Overall differences in Φ_i are marginally significant by habitat for later-successional species (Figure 2.7.2a: $H_{2, 43}$ = 5.62, P = 0.06); pairwise comparisons indicate that Φ_i in primary and secondary forests cannot be distinguished (P > 0.7), but that Φ_i values for later successional species in primary and secondary forest are less than in pasture (both P < 0.00001).

Seeds per recruit also differs by dispersal mode (Figure 2.7.2b). Median dispersed seeds per recruit for wind-dispersed species (1,064) is two orders of magnitude higher than that for animal-dispersed species (12; $H_{2, 43}$ = 3.82, P = 0.05). Data are insufficient for tests of Φ of wind-dispersed species by habitat. However dispersed seeds per recruit for individual animal-dispersed recruits in primary forest, secondary forest, and pasture differ substantially, with Φ in pasture (187) an order of magnitude higher than in forests (10; $H_{2, 43}$ = 12.38, P = 0.002). Pairwise comparisons of Φ_i show marginal differences between primary and secondary forest (P = 0.06), but significant differences of both with pasture (P = 0.0001 and P = 0.02, respectively). It should be noted that all estimates are based on seed fall and seedling recruits of widely scattered dispersed seeds, not dense seedling cohorts under fruiting trees.

2.3.4 Effective seeds per station E_{it}

Number of effective seeds per seed trap E_{it} is generally low (Figure 2.7.3), without a clear signal of habitat differences (P > 0.4). Breakdown by life history and dispersal mode indicate that distributions differ across habitats for comparisons of pioneer and later-successional trees ($H_{5, 43}$ = 17.18, P = 0.01) and for comparisons of animal- and wind-dispersed trees ($H_{5,43}$ = 12.88, P = 0.025). Values are extremely low for all categories in pasture, either from failure of seeds to arrive (later-successional and/or animal-dispersed species) or from enormous numbers of seeds required to produce a recruit due to extreme mortality under extreme conditions (many pioneers, mostly wind-dispersed). Seed mass is unrelated to E_{it} (P > 0.9).

2.3.5 Relative seed effectiveness ε_{it}

Relative seed effectiveness ε_{it} estimates the degree to which a species differs in E_{it} among potential competitors found in seed fall and among recruits, here estimated m^{-2} (Figure 2.9.3). As a composite metric, ε_{it} estimates distributions of success among sites for potentially competing recruits, offering an estimate of relative success by habitat over a year. Here median ε_{it} at almost all sites for most species is nearly zero, with highly skewed distributions that nonetheless differ ($H_{5,1493}$ = 47.40, P < 0.000001). Values for pasture are particularly skewed, reflecting sparse seed fall or massive seed fall with little establishment. Pairwise comparisons of ε_{it} suggest a marginal difference between forest types (P = 0.1), and show clear differences between both forest types and pasture (both P < 0.0001).

Evaluations by life history and dispersal mode are instructive (Figure 2.7.4). Pioneer and later-successional species show substantial differences by habitat ($H_{5,1493}$ = 125.91, P <

0.0001), with higher values for later-successionals in primary forest and for pioneers in secondary forest. Comparisons of ε_{it} by dispersal mode show higher values for animal-dispersed species in primary forest and an uneven pattern for wind-dispersed species ($H_{5,1493} = 171.52$, $P < 0.0001$). As with other measures, rank-order ε_{it} of later-successional species differs in the three habitats (Figure 2.7.4a, both frames $P < 0.00001$). Within a dispersal mode, rank-order of ε_{it} of animal-dispersed seeds differs dramatically by habitat, with much higher values for primary forest than other habitats (Figure 2.7.4b, $P < 0.0001$). Pairwise contrasts of ε_{it} of wind-dispersed species also differs by habitat ($P < 0.0001$), with distributions between primary and secondary forest indistinguishable ($P > 0.8$), but differences between both forest types and pasture highly significant (both $P < 0.00001$).

Plots of relative seed effectiveness ε_{it} by species indicate reasons for highly skewed distributions of life history and dispersal guilds (Figure 2.7.5). In all three habitats, most species have extremely low seed effectiveness relative to seeds of other species with records of both seed fall and establishment. Only three species in primary forest show median ε_{it} much above zero (*Nectandra ambigens, Chamaedorea tepejilote, Cupania glabra*). Other species have a median of zero (at least half the trap stations in which seeds fell recorded no recruits of the species), with total recruits ranging from 1-33 individuals (Table 2.9.1). Whether with high or low seed fall, ten species barely recruit at all, or several seedlings of a species recruit at one or a few stations. Secondary forest is more extreme. Medians, quartiles and ranges indicate only three species (*Psychotria veracruzensis, P. amalago, Cojoba arborea*) have six or more recruits at an appreciable number of stations. *Trichospermum galeottii* has one recruit from a seed fall of > 45,000 seeds, marking an extreme disparity in seeds that arrive and what actually establishes. In pasture, two wind-

dispersed trees (*Eupatorium galeottii, Heliocarpus appendiculatus*) and one animal-dispersed tree (*Trema micrantha*) recruit in the presence of other species at more than a few stations. Ten species show token establishment in the company of other species.

2.4 DISCUSSION

Seeds and seedlings of plants that produce thousands to millions of seeds in a lifetime experience immense mortality; a challenge is to understand how such fortunes differ among species, species characteristics and habitats that species occupy (Salisbury 1943; Harper 1977). Seed effectiveness offers insights that are easily lost in definitional disputes about what constitutes seed limitation as contrasted with recruitment limitation. With emphasis on overall success of seeds in producing established seedlings and juveniles, seed effectiveness subsumes stage-specific mortality and therefore limitation that undoubtedly varies by species, habitat, and local circumstance (Salisbury 1943; Harper 1977).

The idea of counting seeds required to produce recruits is straightforward, but calculation is not. Seed counts are overwhelming at large spatial scales: spot sampling at smaller scales (e.g. $0.5 - 1.0$ m^2) are feasible (Martínez-Garza *et al.* 2009). Records of seedling establishment are also influenced by sampling scale (Kobe & Vriesendorp 2009). For instance, samples of seedlings in a few m^2 near seed traps are adequate for calculating metrics in forest habitats, while juveniles are so infrequent in pastures that sampling requires hundreds of m^2 to record any seedlings at all (Howe *et al.* 2010). If forest sites were sampled on the same scale as pasture (a logistically infeasible alternative), more species would appear. The metric Φ_i, while dimensionless in presentation, is calculated

using appropriate area scales. We standardize to m². Of primary interest in this paper is the nature of distributions of metrics rather than numbers recorded or scales employed.

Failure of seeds to arrive, germination failure, or death of young seedlings limits samples to a small fraction of the total flora. Sparse seed fall and rare recruitment are the rule for most species in similar studies of tropical rainforest. A four-year study in mature forest in Panama yielded 53 species counted as both seeds and seedlings at 200 stations in a forest of approximately 300 tree species (Harms *et al.* 2000). A two-year study in continuous forest in French Guiana yielded 14 out of ~ 600 species with both seeds and seedlings sampled at 160 stations (Norden *et al.* 2009). In the present study, < 1% of 43 species occur both in seed traps (46,807 seeds) and seedling censuses (378 recruits). This is a small sample from ~ 300 tree species in the surrounding Los Tuxtlas complex of forests, with ~ 120 tree species ha^{-1} in forests nearby. Such realities, including extremely sparse recruitment in pasture (not sampled in the studies in Panama or French Guiana), force us to sample seeds and seedlings at different scales and standardize indices of seeds per recruit and seed effectiveness to m² for discussion.

These metrics offer general insights into distributions of realized seed potential: First, relative seed effectiveness ε_{it} is very low for most species in most circumstances. Medians of effective seeds for the majority of species with adequate data in at least one habitat are 0; at least half of the stations at which a species appeared as seed did not record seedlings. Nonetheless, these values overestimate seed success in a forest complex of ~300 tree species. For the vast majority of species, either seed fall or post-dispersal seedling survival is negligible.

As with comparable studies, our measures do not register the vast majority of species, which have either very low seed fall, low seed germination, or low seedling survival at any given site (Muller-Landau *et al.* 2002; Norden *et al.* 2009a). As an extreme example, in secondary forest seed fall of *Eupatorium galeottii* averages > 3,500 m^{-2}, with no establishment (Martínez-Garza *et al.* 2009). In secondary forests 10-20 years old, suitable environment for seedlings of early pioneers no longer exists, reflecting an ontogenetic niche shift from habitats where adults flower and bear seeds to those suitable for establishment (Miriti 2006). Although *E. galeottii* does not register in our calculations in secondary forest, it does register in pasture where > 1,200 seeds are required to produce a recruit. While the odds of seed success of animal-dispersed trees are higher with appropriate dispersal agents than without (Nunez-Iturria, Olsson & Howe 2008; Terborgh *et al.* 2008; Sethi & Howe 2009), at any given time relative seed effectiveness for most species at Los Tuxtlas remains very low even where dispersal agents are common.

Second, the low return on seed fall (high Φ_{it}, low E_{it} and low ε_{it}) admits a strong apparent role for stochastic processes for most species (Hubbell 2001). In our study, relative seed effectiveness predicts recruitment for four species (*Astrocaryum mexicanum, Cupania glabra, Chamaedorea tepejilote, Nectandra ambigens*) in primary forest. The probability that a seed will produce a seedling for other species is low; for many species, recruitment is negligible except when vagaries of chance play a major role. This does not deny a role for deterministic processes that favor certain species that establish in soils of a particular type or drainage some of the time (Norden *et al.* 2009a). Even in the latter study, an exceptionally thorough investigation, the variance that can be attributed to abiotic factors is low for the 14 species for which data are available. In substantially more diverse terra-

firma forests in the western Amazon, where the greater majority of > 1000 tree species occur in densities of one in 1-10 hectares (Pitman *et al.* 2001; Terborgh *et al.* 2002), the role of chance in determining where seeds land and seedlings survive is likely immense for many tree species most of the time.

Third, species composition of recruits common enough to be sampled overlaps little among the three adjacent habitats. An earlier study shows that tree species in the seed rain of primary and secondary forest overlap substantially, but that seeds falling in pasture represent a different sample of both pioneer and later-successional taxa (Martínez-Garza *et al.* 2009). In the present study, the 13 and 14 tree species in primary and secondary forest for which Φ_i and E_{it} can be calculated share four species, while the 14 and 13 species in secondary forest and pasture share three. Of shared species, seeds and seedlings of *Cupania glabra* and *Piper amalago* are present in all three habitats. *Cupania glabra* had the highest relative seed effectiveness (ε_{it}) in primary forest, was notable in secondary forest, and showed only token effectiveness in pasture. *Piper amalago* had very low relative effectiveness in all three habitats. Many more species occur in each forest habitat, but do not occur in both seed and recruit samples for the year studied. In any given year, recruitment is skewed in favor of a few species and sparse or negligible for others.

Fourth, seed effectiveness has implications for conservation and restoration in diverse tropical communities. Skewed species-abundance distributions of tree species means that the vast majority of species are infrequent to rare, are likely to have very low relative seed effectiveness, and are vulnerable to local population failure when already sparse populations are reduced by chance reductions in dispersal or seedling survival. Vulnerability of rare species in log-normal or otherwise highly skewed species-abundance

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distributions is a central assumption of the theory of island biogeography (MacArthur 1972; Hurtt & Pacala 1995). We predict that low seed effectiveness predicts local loss of species in isolated habitat fragments or forest restorations (Maina & Howe 2000). The component of chance dispersal of seeds and chance survival of seedlings means that community restoration best begins with plantings of robust seedlings with less variance in survival than seeds or small seedlings (see Howe & Miriti 2004; Martinez-Garza *et al.* 2005). Where a restoration goal is to attract species from surrounding forests, high values of seeds per recruit, low seed effectiveness, and vagaries of disperser behavior increase the likelihood that species composition will by chance differ widely from one synthetic forest to another.

Finally, changes in these metrics over time are likely to differ within and between habitats. Primary forests may well vary in which species have high or low dispersal and high or low establishment limitation coincident with slight variations in annual fruit production, with tree-fall gaps, or in response to the regular environmental rhythms of El Niño and La Niña. However, one does not expect differences in the shapes of effectiveness distributions, even if the species scoring high or low change from one year to another. Older secondary forests will reflect the same kinds of adjustments in addition to directional changes as succession proceeds, evidenced by increasing effectiveness of later-successional species at the expense of others. The snapshot of dispersal and establishment limitation in pasture a year after fencing is a unique representation of a rapidly-changing phase of secondary succession; species composition and median community metrics of Φ, E and ε will change annually as planted trees in this experiment mature, cast shade, suppress grasses, and produce conditions favorable to shade-tolerant seedlings. Dispersal

and establishment limitation will probably approach and soon parallel those in older forests, leading to a homogenization of community values of Φ_i, E_{it} and ε_{it}, and ultimately of community composition (Kanagaraj *et al.* 2011). One expects more variation between years in the recruit template of early successional than later successional habitats. Annual variations in local weather, El Niño and La Niña cycles and the rarity of most recruiting species may create quite different multi-species seedling cohorts in early succession. It is likely that the seedling and juvenile templates of later-successional species for future forest communities will appear more stochastic from one year to another and from one site to another in just-abandoned pasture than in existing forest.

Caveats are in order. Measures of Φ_i, E_{it} and ε_{it} may be affected by pre-existing seed and seedling banks. Seeds per recruit potentially under-estimates primary and secondary forest values for species with significant seedling banks and to lesser degree seed banks, thereby over-estimating seed effectiveness. We doubt that this is important for most species in our forest samples because most tropical seeds germinate or die within weeks of arrival (Norden *et al.* 2009b), and by inspection most species with seeds both falling in seed traps and counted as seedlings are uncommon or rare as seedlings or saplings in surrounding forest. Exceptions to this rule in primary and secondary forest are *Astrocarym mexicanum, Nectandra ambigens,* and *Trichilia martiana*, for which seedlings are evident in the area. Calculations probably under-estimate Φi for these three species. Seeds of some pioneer species in our samples (e.g. *Cecropia obtusifolia, Trema micrantha, Trichospermum galeottii*) may remain dormant in soil for months to years (Dalling & Denslow 1997). This in theory could inflate *C. obtusifolia* and *T. micrantha* effectiveness in pasture, though ε_{it} for

both are low. In secondary forest, possible influence of seed dormancy on *T. galeottii*

measures are overwhelmed by extremely high seed fall with virtually no recruitment.

2.5 CONCLUSIONS

To answer the question in the title, seed potential for many species is far more apparent

than real. The ratio of seeds per recruit is often high, while relative seed effectiveness is

usually very low. Quantitative measures that integrate results of seed arrival and survival

in tropical habitats - of seeds per recruit, seed effectiveness, and relative seed effectiveness

- underscore both the vast differences in realized regeneration potential for tropical trees,

and that in a given habitat very few species contribute much to seedling communities at a

given place and time. Notably, negligible effectiveness in actually producing recruits for

seeds of most species in most locations is a confirmation of the view that seed and seedling

mortality strongly limit effective plant reproduction within primary and secondary forest,

and even more severely limit recruitment in pasture recently released from grazing.

2.6 LITERATURE CITED

Aide,T. M., Zimmerman, J., Herrera, L., Rosario, M. & Serrano, M. (1995) Forest recovery in abandoned tropical pastures in Puerto Rico. *Forest Ecology and Management*, 77, 77-86.

Bongers, F., Popma, J., Meave-del-Castillo, J. & Carabias, J. (1988) Structure and floristic composition on the lowland rain forest of Los Tuxtlas, Mexico. *Vegetation,* 74, 55-80.

Clark, C.J., Poulsen, J.R., Levey, D.J. & Osenberg, C.W. (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist,* 170, 128-142.

Clark, J.S. (1998) Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. *American Naturalist,* 152, 204-224.

Colwell, R.K. (2006) EstimateS: statistical estimation of species richness and shared species from samples. *Version 8.0 User's Guide and application*. published at: http://viceroy.eeb.uconn.edu/estimates. .

Chazdon, R.L. (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science,* 320, 1458-1460.

Dalling, J.W. & Denslow, J.S. (1997) Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. *Journal of Vegetation Science,* 9, 669-678.

Dalling, J.W., Hubbell, S.P. & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, 86, 674-689.

Darwin, C. (1859) *On the origin of species by means of natural selection*. J. Murray, London,.

González Soriano, E., Dirzo, R. & Vogt, R.C. (1997) *Historia natural de los Tuxtlas,* 1. edn. Universidad Nacional Autónoma de México Instituto de Ecología, México.

Harms, K.E. & Dalling, J.W. (1997) Damage and Herbivory Tolerance Through Resprouting as an Advantage of Large Seed Size in Tropical Trees and Lianas. *Journal of Tropical Ecology,* 13, 617-621.

Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature,* 404, 493-495.

Harper, J.L. (1977) *Population biology of plants*. Academic Press, London ; New York.

Holl, K.D. (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica,* 31, 229-242.

Howe, H.F. & Miriti, M.N. (2004) When seed dispersal matters. *Bioscience,* 54, 651-660.

Howe, H.F., Urincho-Pantaleon, Y., de la Peña-Domene, M. & Martinez-Garza, C. (2010) Early seed fall and seedling emergence: precursors to tropical restoration. *Oecologia,* 164, 731-740.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & de Lao, S.L. (1999) Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. *Science,* 283, 554-557.

Hurtt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation - reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology,* 176, 1-12.

Ibarra-Manriquez, G. & Sinaca, S. (1995) Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México. *Revista de Biología Tropical,* 43, 75-115.

Ibarra-Manriquez, G. & Sinaca, S. (1996a) Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Mimosaceae a Verbenaceae). *Revista de Biología Tropical,* 44, 41-60.

Ibarra-Manriquez, G. & Sinaca, S. (1996b) Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Violaceae a Zingiberaceae). *Revista de Biología Tropical,* 44, 427-447.

Ingle, N.R. (2003) Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia,* 134, 251-261.

Kanagaraj, R., Wiegand, T., Comita, L.S. & Huth, A. (2011) Tropical tree species assemblages in topographical habitats change in time and with life stage. *Journal of Ecology,* 99, 1441-1452.

Kitajima, K. (2002) Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Functional Ecology,* 16, 433-444.

Kobe, R.K. & Vriesendorp, C.F. (2009) Size of sampling unit strongly influences detection of seedling limitation in a wet tropical forest. *Ecology Letters,* 12, 220-228.

MacArthur, R.H. (1972) *Geographical ecology; patterns in the distribution of species*. Harper & Row, New York,.

Maina, G.G. & Howe, H.F. (2000) Inherent rarity in community restoration. *Conservation Biology,* 14, 1335-1340.

Martínez-Garza, C., Flores-Palacios, A., De La Peña-Domene, M. & Howe, H.F. (2009) Seed rain in a tropical agricultural landscape. *Journal of Tropical Ecology,* 25, 541-550.

Martínez-Garza, C. & González-Montagut, R. (1999) Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. *Plant Ecology,* 145, 255-265.

Martinez-Garza, C., Pena, V., Ricker, M., Campos, A. & Howe, H.F. (2005) Restoring tropical biodiversity: Leaf traits predict growth and survival of late-successional trees in early-successional environments. *Forest Ecology and Management,* 217, 365-379.

Martínez-Ramos, M. (1985) Claros, ciclos vitales de los arboles tropicales y regeneración natural de las selvas altas perennifolias. *Investigaciones sobre la Regeneración de selvas altas en Veracruz, México.* (eds A. Gómez-Pompa & S. Del-Amo), pp. 191-240. Alhambra Mexicana S.A. de C.V., Mexico City.

Miriti, M.N. (2006) Ontogenetic shift from facilitation to competition in a desert shrub. *Journal of Ecology,* 94, 973-979.

Moles, A.T., Falster, D.S., Leishman, M.R. & Westoby, M. (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology,* 92, 384-396.

Muller-Landau, H.C., Wright, S.J., Calderón, O., Hubbell, S.P. & Foster, R.B. (2002) Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. *Seed Dispersal and Frugivory* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 35-53. CAB International, Wallingford.

Nepstad, D.C., Uhl, C., Pereira, C.A. & daSilva, J.M.C. (1996) A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos,* 76, 25-39.

Norden, N., Chave, J., Belbenoit, P., Caubere, A., Chatelet, P., Forget, P.M., Riera, B., Viers, J. & Thebaud, C. (2009a) Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. *Journal of Ecology,* 97, 186-197.

Norden, N., Daws, M.I., Antoine, C., Gonzalez, M.A., Garwood, N.C. & Chave, J. (2009b) The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. *Functional Ecology,* 23, 203-210.

Nunez-Iturria, G., Olsson, O. & Howe, H.F. (2008) Hunting reduces recruitment of primate-dispersed trees in Amazonian Peru. *Biological Conservation,* 141, 1536-1546.

Pitman, N.C.A., Terborgh, J.W., Silman, M.R., Nunez, P., Neill, D.A., Ceron, C.E., Palacios, W.A. & Aulestia, M. (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology,* 82, 2101-2117.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martínez-Ramos, M., Mazer, S.J., Muller-Landau, H.C., Pena-Claros, M., Webb, C.O. & Wright, I.J. (2008) Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology,* 89, 1908-1920.

Popma, J., Bongers, F. & Werger, J.A. (1992) Gap-dependence and leaf characteristics of trees in a tropical lowland rain forest in México. *Oikos,* 63, 207-214.

Rudel, T.K., Coomes, O.T., Moran, E., Achard, F., Angelsen, A., Xu, J.C. & Lambin, E. (2005) Forest transitions: towards a global understanding of land use change. *Global Environmental Change-Human and Policy Dimensions,* 15, 23-31.

Salisbury, E.J. (1943) The reproductive capacity of plants. *Journal of Ecology,* 31, 44-47.

Schupp, E.W., Howe, H.F., Augspurger, C.K. & Levey, D.J. (1989) Arrival and survival in tropical treefall gaps. *Ecology,* 70, 562-564.

Schupp, E.W., Jordano, P. & Gomez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist,* 188, 333-353.

Sethi, P. & Howe, H.F. (2009) Recruitment of Hornbill-Dispersed Trees in Hunted and Logged Forests of the Indian Eastern Himalaya. *Conservation Biology,* 23, 710-718.

Svenning, J.C. & Wright, S.J. (2005) Seed limitation in a Panamanian forest. *Journal of Ecology,* 93, 853-862.

Swamy, V., Terborgh, J., Dexter, K.G., Best, B.D., Alvarez, P. & Cornejo, F. (2011) Are all seeds equal? Spatially explicit comparisons of seed fall and sapling recruitment in a tropical forest. *Ecology Letters,* 14, 195-201.

Terborgh, J., Loayza, P.A., Dexter, K., Cornejo, F. & Carrasco, C. (2011) Decomposing dispersal limitation: limits on fecundity or seed distribution? *Journal of Ecology*, no-no.

Terborgh, J., Nunez-Iturri, G., Pitman, N.C.A., Valverde, F.H.C., Alvarez, P., Swamy, V., Pringle, E.G. & Paine, C.E.T. (2008) Tree recruitment in an empty forest. *Ecology,* 89, 1757-1768.

Terborgh, J., Pitman, N., Silman, M.R., Schichter, H. & Nunez, V.P. (2002) Maintenance of tree diversity in tropical forests. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation.* (ed. D.J. Levey, Silva, W. R. ,&. Galetti, M.), pp. 1-17. CAB International, Wallingford.

Uhl, C. (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. *Journal of Ecology,* 75, 377-407.

Wright, S.J., Muller-Landau, H.C., Calderon, O. & Hernandez, A. (2005) Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology,* 86, 848-860.

Zimmerman, J.K., Pascarella, J.B. & Aide, T.M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology,* 8, 350-360.

2.7 FIGURES
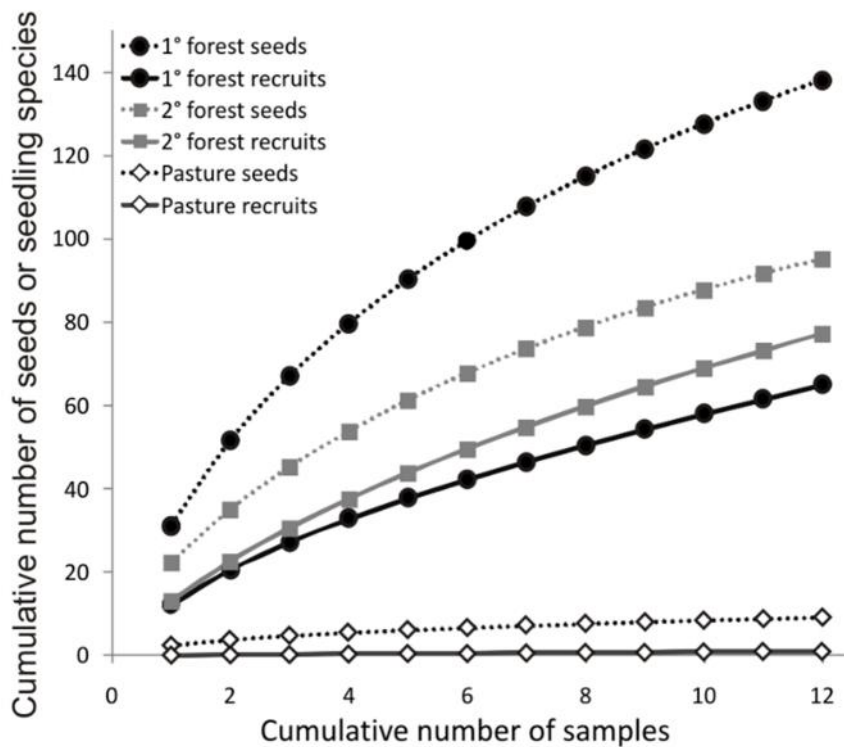
Figure 2.7.1. Species accumulation (Mao Tau) of seed and recruit samples up to 24 months after planting. Each sample is a species count in 1-m^2 seed trap (for seeds) and 5 adjacent m^2 (for seedlings), with 12 samples of each per habitat per census. For the purpose of metrics (Table 2.8.1), the sample area for pasture is increased as indicated in the text.
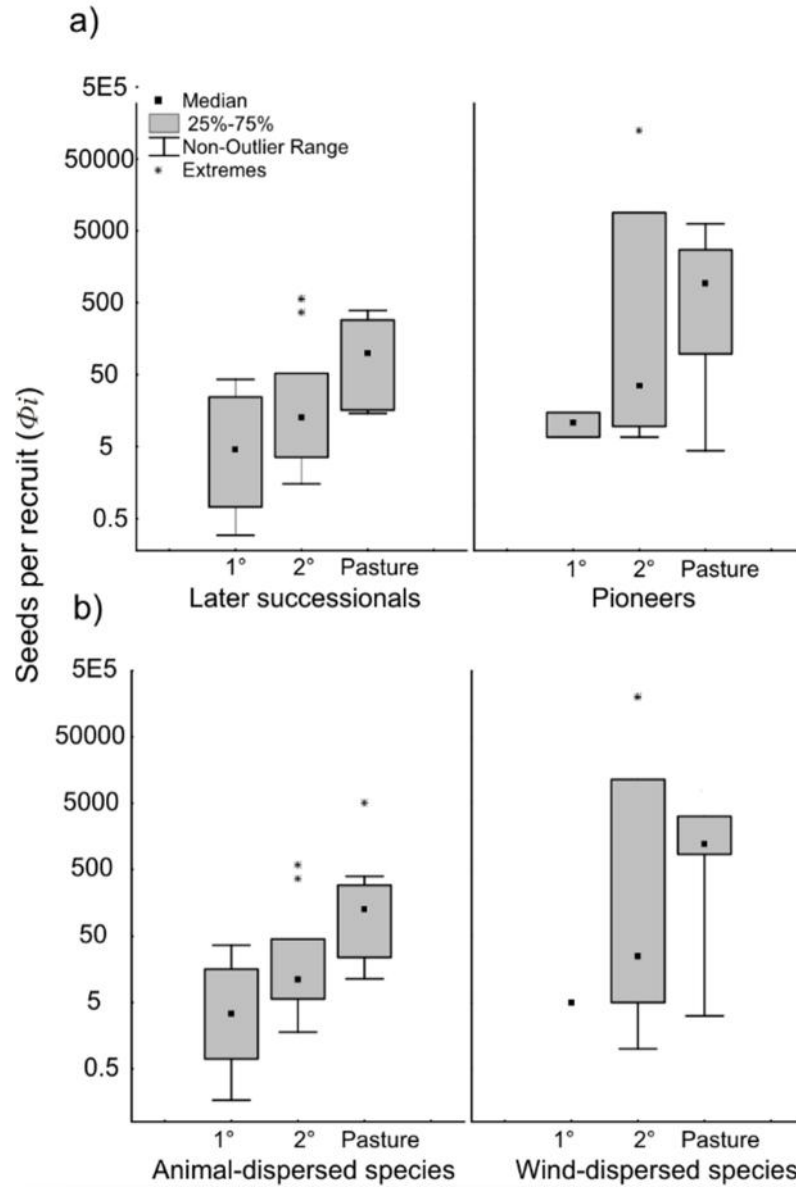
Figure 2.7.2. Seeds per recruit (Φi) as a function of life history, dispersal mode, and habitat. Medians, quartiles and ranges illustrate Φ_i in: (a) later-successional and pioneer species as a function of habitat, and (b) animal- and wind-dispersed species as a function of habitat. See text for statistics.
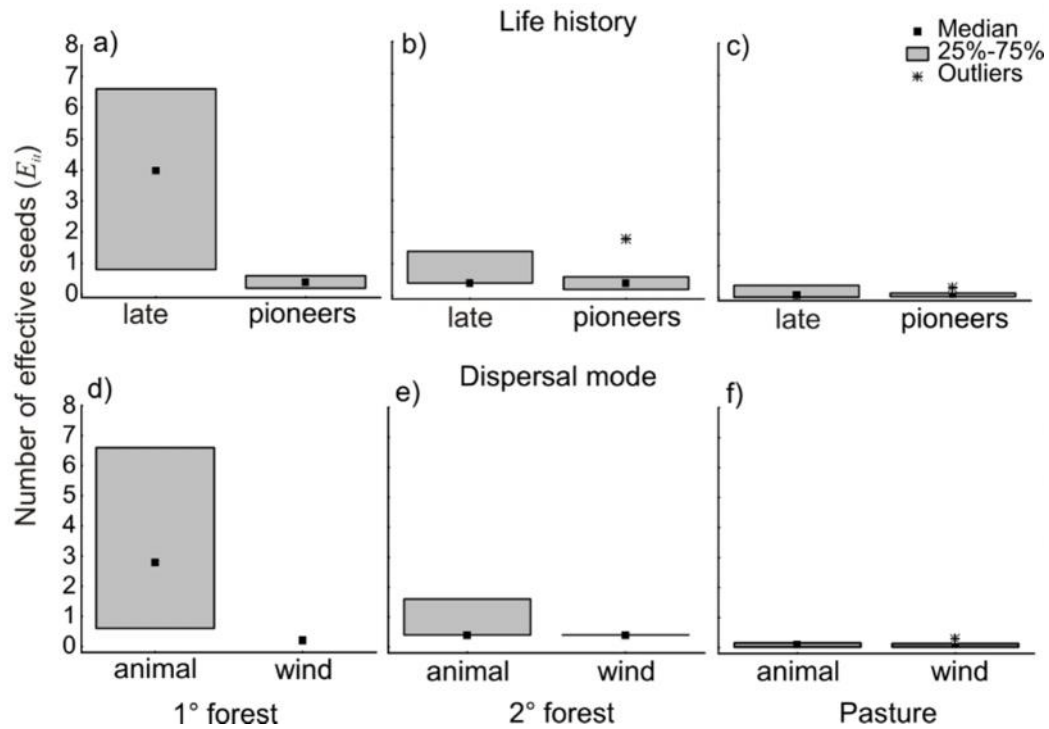
Figure 2.7.3. Effective seeds per trap (E) reflects those seeds of a species that actually produce recruits in a particular time and place, here in m² for illustration: (a) Medians and quartiles of later-successionals and pioneers as a function of habitat, and (b) medians and quartiles of animal- and wind-dispersed species as a function of habitat. See text for statistics.
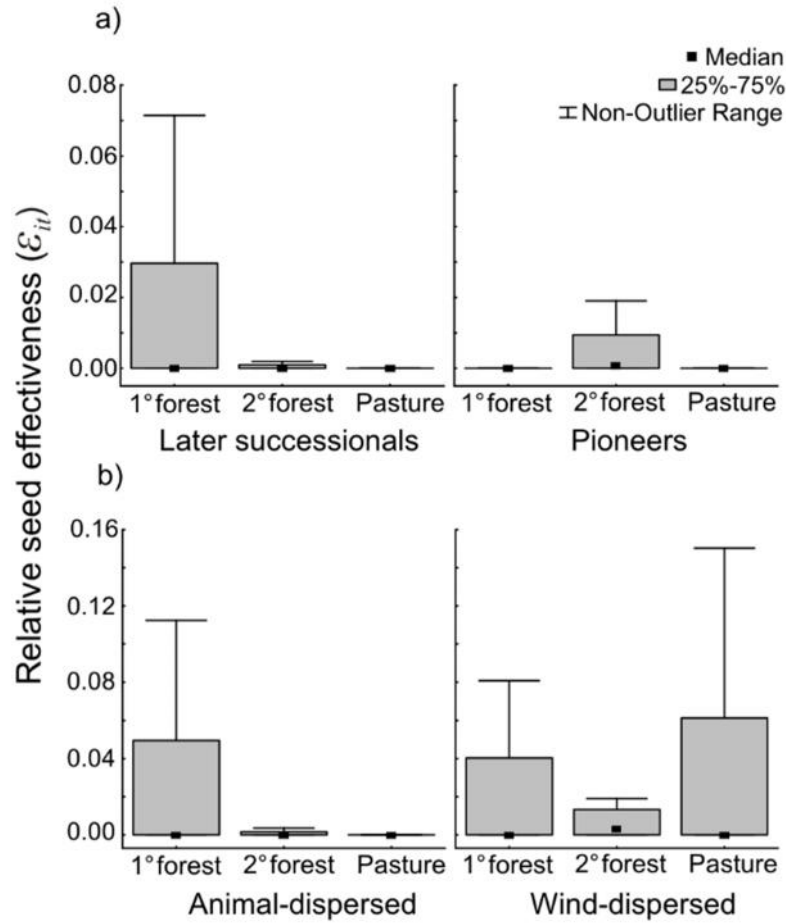
Figure 2.7.4. Relative seed effectiveness (ε_i t) by life-history status and dispersal mode for primary and secondary forest and pasture: (a) pioneers and later-successionals by habitat, and (b) animal- and wind-dispersed species by habitat. See text for statistics.
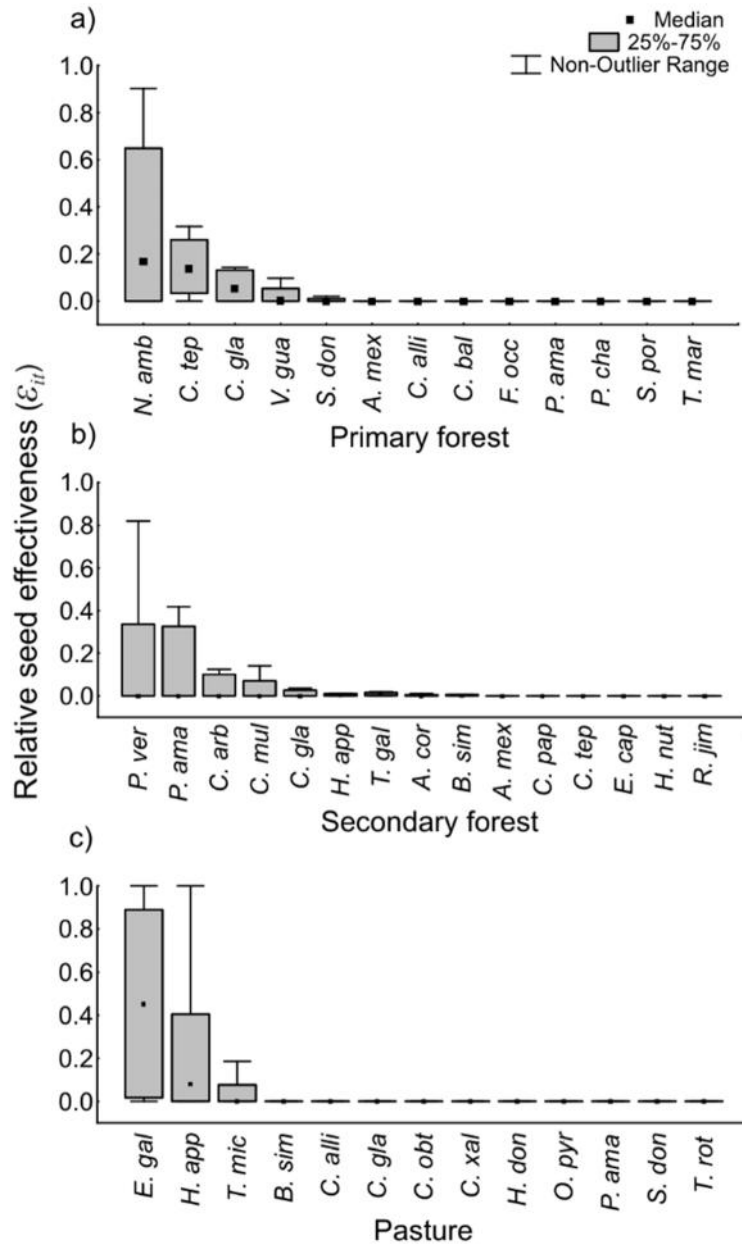
Figure 2.7.5. Rank order of median εit of trees in three habitats: (a) Primary forest: *Nectandra ambigens, Chamaedorea tepejilote, Cupania glabra, Virola guatemalensis, Stemmadenia donnell-smithii, Astrocaryum mexicanum, Cordia alliodora, Cymbopetalum baillonii, Faramea occidentalis, Piper amalago, Psychotria chapensis, Sideroxylon portoricense, Trichilia martiana,.* (b) Secondary forest: *Psychotria veracruzensis, Piper amalago, Cojoba arborea, Cnidoscolus multilobus, Cupania glabra, Heliocarpus appendiculatus, Trichospermum galeottii, Acacia cornigera, Bursera simaruba, Astrocaryum mexicanum, Carica papaya, Chamaedorea tepejilote, Eugenia capuli, Hampea nutricia, Rollinia jimenezii,* (c) Pasture species: *Eupatorium galeottii, Heliocarpus appendiculatus, Trema micrantha, Bursera simaruba, Cordia alliodora, Cupania glabra, Cecropia obtusifolia, Conostegia xalapensis, H. donnell-smithii, Ochroma pyramidale, Piper amalago, Stemmadenia donnell-smithii, Tetrorchidium rotundatum.*

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2.8 TABLES

Table 2.8.1. Definition of terms, calculated within habitat or over all habitats.

_____

Seeds per recruit, Φi, is the number of seeds of species i needed for 1 recruit:

$$\Phi_i = \frac{A \cdot S_i}{R_i} \qquad i = 1, 2, \ldots, n$$

where S_i is the total seeds of species i that fall in a trap in a habitat, R_i is the total number of recruits of species i in a habitat, and A is the ratio of recruitment area sampled (m²) in a habitat divided by the area sampled by seed traps in a habitat.

Effective seeds of individual species i per individual trap t are computed as:

$$E_{it} = S_{it} \cdot \left(\frac{1}{\Phi_i}\right) \qquad i = 1, 2, \ldots, n \; ; \quad t = 1, 2, \ldots, m$$

where S_{it} is the number of conspecifics of species i in a trap t, n is the total number of species in trap t (e.g. 1 or 5 in a given trap), and m is the number of traps (e.g. 12 in primary forest, 96 in pasture).

Relative seed effectiveness ε_{it} is the proportion of effective seeds of species i in trap t among

effective seeds of all species 1, 2, ..., n_{tot} per trap t:

$$\varepsilon_{it} - \frac{E_{it}}{F_{1t} + F_{2t} + \ldots + F_{nt}} \qquad i - 1, 2, \ldots, n \; ; \; t - 1, 2, \ldots, m$$

where ε_{it}, is the relative seed effectiveness of each species in one of the three   habitats.

_____

2.9 APPENDIX

Table 2.9.1. Seed mass and components of seeds per recruit (Φ_i).

	Seed mass (g)	S_i	r_i	Φ_i	Life history	Dispersal mode
Primary forest						
Astrocaryum mexicanum	3.4220	3	33	0.45	Late	Animal
Chamaedorea tepejilote	0.1750	26	37	3.51	Late	Animal
Cordia alliodora	0.0330	1	1	5.00	Pioneer	Wind
Cupania glabra	0.1900	30	14	10.71	Late	Animal
Cymbopetalum baillonii	0.3335	1	4	1.25	Late	Animal
Faramea occidentalis	0.3000	5	26	0.96	Late	Animal
Nectandra ambigens	1.8000	13	220	0.30	Late	Animal
Piper amalago	0.0015	7	3	11.67	Pioneer	Animal
Psychotria chapensis	0.2100	2	3	3.33	Late	Animal
Stemmadenia donnell-smithii	0.0700	7	1	35.00	Late	Animal
Sideroxylon portoricense	0.5423	7	1	20.00	Late	Animal
Trichilia martiana	0.2364	1	29	0.17	Late	Animal
Virola guatemalensis	0.1962	73	10	36.50	Late	Animal
TOTAL		169	246			
Secondary forest						
Acacia cornigera	0.0760	8	2	20.00	Pioneer	Wind
Astrocaryum mexicanum	3.4220	2	1	10.00	Late	Animal
Bernoullia flammea	0.3300	1	5	1.00	Late	Wind
Bursera simaruba	0.1170	148	2	370.00	Late	Animal
Carica papaya	0.0230	9	1	45.00	Pioneer	Animal
Chamaedora alternans	0.1750	5	14	1.79	Late	Animal
Cnidosculus multilobus	0.0800	18	2	45.00	Late	Animal
Cojoba arborea	0.8500	36	6	30.00	Pioneer	Wind
Cupania glabra	0.1900	236	2	590.00	Late	Animal
Eugenia capuli	0.0560	1	2	2.50	Late	Animal
Hampea nutricia	0.1100	3	3	5.00	Pioneer	Wind
Heliocarpus appendiculatus	0.0015	4,574	2	11,435.00	Pioneer	Wind
Piper amalago	0.0015	13	9	7.22	Pioneer	Animal
Psychotria veracruzensis	0.0020	9	8	5.63	Late	Animal
Rollinia jimenezii	0.1600	5	2	12.50	Late	Animal
Trichospermum galeottii	0.0030	40,319	1	201,595.00	Pioneer	Wind
TOTAL		45,387.00	62.00			
Pastures						
Bursera simaruba	0.1170	7	104	11.38	Late	Animal
Cecropia obtusifolia	0.0010	31	28	187.11	Pioneer	Animal
Conostegia xalapensis	0.0001	12	23	88.17	Pioneer	Animal
Cordia alliodora	0.0330	1	54	3.13	Pioneer	Wind
Cupania glabra	0.1900	7	3	394.33	Late	Animal
Eupatorium galeotti	0.0009	167	22	1282.86	Pioneer	Wind

Hampea nutricia	0.1100	7	1	1183.00	Pioneer	Wind
Heliocarpus appendiculatus	0.0015	376	20	3177.20	Pioneer	Wind
Heliocarpus donnell-smithii	0.0010	184	4	7774.00	Pioneer	Wind
Ochroma pyramidale	0.0080	5	1	845.00	Pioneer	Wind
Piper amalago	0.0015	1	5	33.80	Pioneer	Animal
Stemmadenia donnell-smithii	0.0700	1	1	169.00	Late	Animal
Tetrorchidium rotundatum	0.0480	2	24	14.08	Late	Animal
Trema micrantha	0.0070	457	15	5148.87	Pioneer	Animal
TOTAL		1251	70			

Where s_i is total seeds collected of species i in traps in a habitat, r_i is total recruits of species i in adjacent habitat, and Φi is the number of seeds per recruit, standardized on a m² scale. Guild categories are life history (pioneer or late successional) and dispersal mode (animal or wind). Checklist in Gonzalez-Soriano, E., Dirzo, R., & Vogt, R. C. Editors. (1997). *Historia Natural de Los Tuxtlas.* Universidad Nacional Autónoma de México. Mexico City, Mexico.
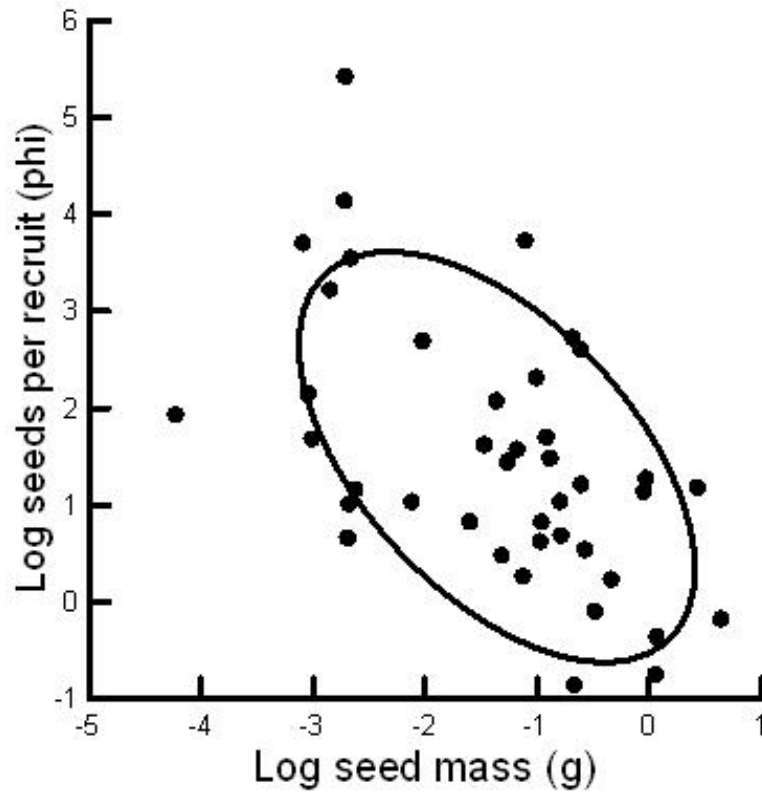
Figure 2.9.1 Negative correlation of log10 seeds per recruit (Φi) with increasing log seed mass (g) (r = - 0.55, p < 0.001). The ellipse is expected to include 68% of samples.
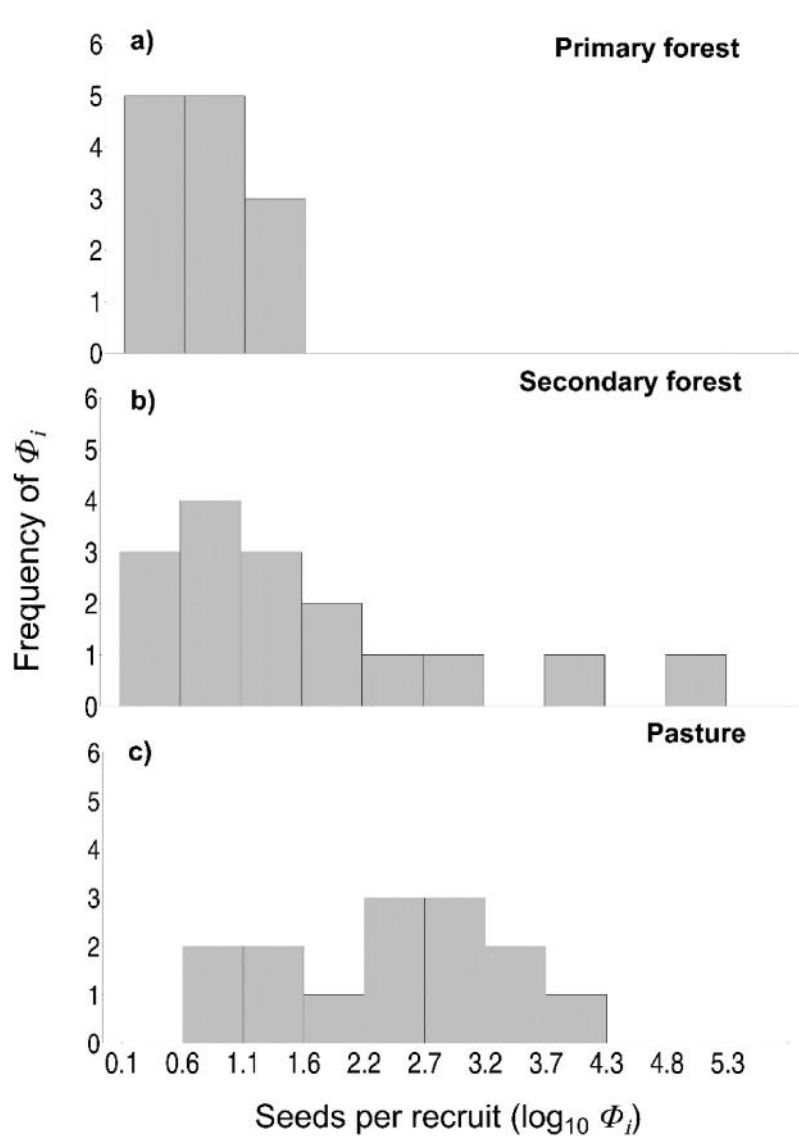
Figure 2.9.2. Frequency distributions of seeds per recruit (Φi) among primary forest, secondary forest, and recently abandoned pasture habitats at Los Tuxtlas, Veracruz, Mexico. Log10 (seeds per recruit +1) accommodates realized untransformed Φi values up to 202,000. Note differences in scale on the y-axes. See text for statistics.
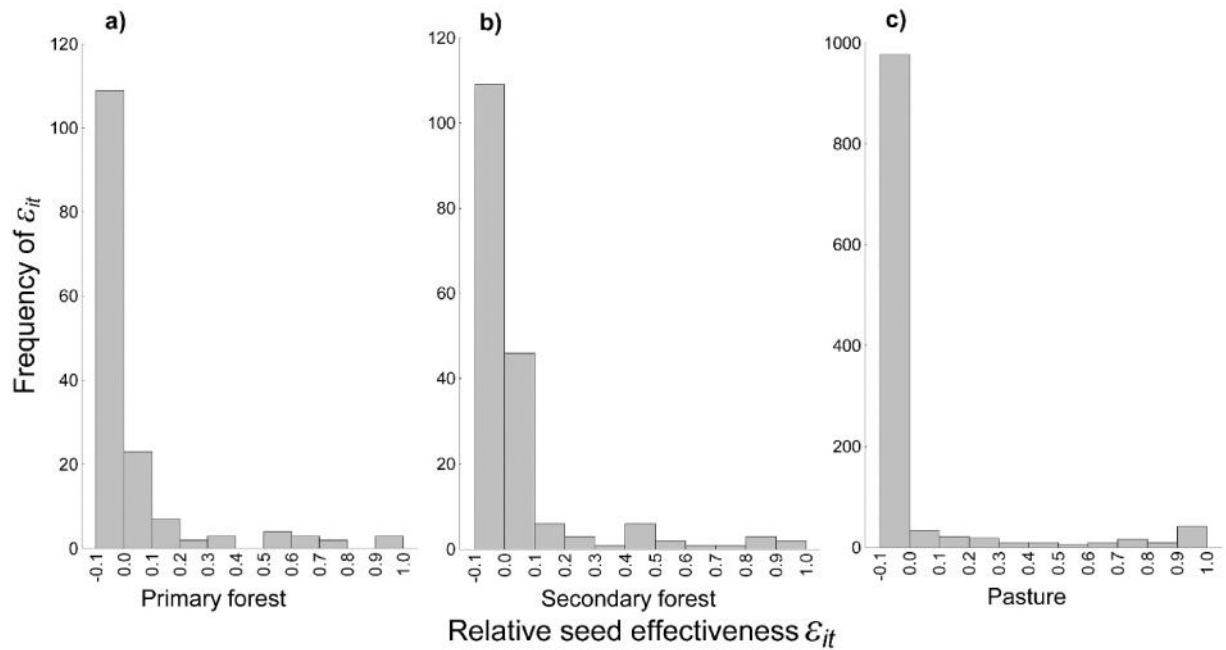
Figure 2.9.3. Frequency distributions of relative seed effectiveness εit of species arriving and surviving at a seed trap and surroundings. All distributions are highly skewed, with most stations reflecting very low relative seed effectiveness for most species. Differences in rank order of εit for primary and secondary forests are marginally significant; those between the two forest types and pasture highly significant. Differences in scale of the y-axis for pasture compared with forest habitats are due to large numbers of samples with very low εit in abandoned pasture plots. See text for statistics.

CHAPTER III

3. EARLY RECRUITMENT DYNAMICS IN TROPICAL RESTORATION

Early recruitment dynamics in tropical restoration

Marinés de la Peña-Domene, Cristina Martínez-Garza and Henry F. Howe

3.1 INTRODUCTION

The relationship between deforestation and forest regeneration will determine the future

of tropical biomes. Tropical forests have the highest biodiversity of all terrestrial

ecosystems (Turner 1996, Dirzo 2001), yet total deforestation and forest fragmentation are

rapidly destroying much of the remaining old-growth forest between the Tropic of

Capricorn and the Tropic of Cancer (Houghton 1994, Ojima et al. 1994, Bryant et al. 1997,

Fearnside 1999, Fahrig 2003). Less appreciated is the rapid growth of secondary forest on

land that has been abandoned (Chazdon 2003, Rudel et al. 2005, Wright 2010). Assisted

regeneration and full-scale forest restoration have potentially important roles in regaining

lost biodiversity and ecosystem services. A challenge, addressed here, is to test means of

accelerating re-vegetation of patches to connect forest fragments in permanent agricultural

mosaics where substantial land area will not be abandoned to natural succession or set

aside for ecological restoration.

Natural succession occurs at different rates under different circumstances. Succession is

slower in abandoned pasture than on land with histories of subsistence agriculture, or

logged areas that are allowed to recover without further disturbance (Aide et al. 1995).

High-intensity, long-term cattle ranching slows ecosystem capacity to recover biodiversity

(Uhl et al. 1988, Nepstad et al. 1991, Jones et al. 2003, Myster 2004, Benítez-Malvido and

Lemus-Albor 2005, Martínez-Garza et al. 2009, Tobon et al. 2011). Depleted seed banks,

compacted soil, depleted soil nutrients, intense solar radiation, low seed input, and high

rates of seed and seedling predation limit re-colonization and growth by late-successional forest trees. Pastures under continued cattle grazing do not regenerate forest.

The rate of recovery of forest richness in abandoned pasture is influenced by dispersal mode and life history of colonizing plants. Small seeds carried long distances by wind, often of a few ubiquitous species, arrive unassisted in disturbed areas (Janzen 1988, Ingle 2003, Howe et al. 2010). A paradox and a challenge for recovery of tropical diversity on badly degraded land is that the great majority of tropical rain-forest trees and shrubs are dispersed by animals (e.g. Frankie et al. 1974, Howe 1977, Howe and Smallwood 1982, and others), yet many birds and mammals of the forest interior avoid crossing open areas, or require unusual motivation to do so. Most animal-dispersed seeds of forest interior do not arrive in extensive pastures until their dispersal agents seek cover or food in isolated trees or small stands of trees (Estrada and Coates-Estrada 2001, 2005). A generalization across the tropics seems to be that large open areas of grasses on thin, eroded soils are slow to recover by unassisted succession because of severe dispersal limitation and adverse conditions for seeds and germinating seedlings.

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

succession. Another question, to be addressed as our experimental plantings mature, is whether recruitment differs in different kinds of plantings.

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

3.2 METHODS

3.2.1 Study area and species

This study was conducted at Los Tuxtlas, Veracruz, Mexico (18˚05′18 y 18˚45′ N, 94˚35′ y 95˚30′ W). The Los Tuxtlas forest of 3,300 km² ranges in elevation from 200 to 1,700 m a.s.l. (Dirzo et al. 1997). This volcanic region is characterized by acidic soils (pH 4.9) with a large clay component(48.5% clay), having formed from basaltic and andesitic rock mixed with volcanic ash (4.9, Guevara et al. 2004). Records of the Los Tuxtlas Biological Station of the

Universidad Nacional Autónoma de México show mean annual precipitation of 4825 mm

per year from 1997 to 2006 (unpublished data), a rainy season from June to February and a

dry season from March to May, and a mean annual temperature of 25º C (see Soto and

Gama1997). The formerly forested land in which our plots were established has been

under intensive cattle ranching for at least 30 years on ground planted with native

(*Axonopus compressus* and *Paspalum conjugatum*) and exotic (*Cynodon dactylon*, *Brachiaria*

brizantha, *Brachiaria decumbens* and *Panicum* spp.) grasses. Soil depth ranges from 5 – 72 cm

over volcanic rock, with a mean depth of 26.8 $\pm$ 14.2 SD cm (Martínez-Garza et al. 2011).

Nearby forest holds ~ 300 native tree species (Ibarra-Manriquez and Sinaca 1995, Ibarra-

Manriquez and Sinaca 1996a, b). In Los Tuxtlas landscapes, 81% of 364 sampled plant

species occur in fragments < 5 ha; 58% of species in small fragments in even the most

highly fragmented areas are old-growth trees (Arroyo-Rodríguez et al. 2008). More than

150 fruit-eating birds and mammals occupy the Los Tuxtlas landscape (Estrada et al. 1993),

with wide-ranging fruit-eating bats (e.g. *Artibeus* spp., *Sturnira* spp.) and birds (*Dryocopus*

lineatus, *Gymnostinops montezuma*, *Psilorhinus morio*, *Ramphastos sulfuratus*) among the most

likely dispersal agents of seeds arriving in our developing planted stands.

Planted and recruited species were classified as pioneer or later-successional, and animal-

dispersed or wind-dispersed. Life-history designations are problematic where authors

place the same species in different categories and use several categories (pioneer vs.

persistent; early pioneer, late pioneer, vs. late successional; pioneer vs. old-growth;

generalist vs. specialist; e.g. Martinez-Ramos 1985, Purata 1986, Ibarra-Manriquez and

Oyama 1992, Arroyo-Rodríguez et al. 2008, Chazdon et al. 2011). Because the data at hand

do not lend themselves to statistical distinctions of pasture recruits into several categories

(cf. Chazdon et al. 2011 for secondary and primary forests), we use demographic and associational analyses from the Los Tuxtlas region to categorize species as "pioneers"common in early succession and other "later-successionals" (e.g. Purata 1986, Ibarra-Manriquez and Oyama 1992). This parallels the distinction by Arroyo-Rodríguez et al. (2008) and Howe et al. (2010) between pioneer and old-growth species.

Distinction of animal- and wind-dispersed species is straightforward. Animal-dispersed species are those with fleshy fruits with pulp surrounding seeds as drupes, berries, pomes, deshiscent capsules or indeshiscent pods, as compared with wind-dispersed seeds with wings, balloons, plumes or other structures that greatly increase surface to volume ratios (e.g. Howe and Smallwood 1982, van der Pijl 1982). Species with fruit structures consistent with water dispersal, ballistic dispersal, or hard nuts hoarded by rodents or dispersed by gravity are not present in the sample. Seeds are often re-dispsersed by secondary agents, but rodents likely to carry seeds substantial distances (e.g. the agouti, *Dasyprocta mexicana*) are not present in the plots.

3.2.2 Experiment

In June 2006 we established 24 cattle exclusion plots arrayed in a 3 x 8 grid in 12 ha of active pasture with a slope from 180 to 260 m asl. Remnant trees were removed during site preparation. Each 30×30 m plot was subdivided into four 13×13 m subplots available for seedling establishment, with 2 m crossed central aisles clear of woody vegetation and 1 m external edge cleared by cattle reaching through fences (Figure 3.6.1). Plots were defined with living fences of barbed wire fastened to living poles of *Gliricidia sepium* (Fabaceae), a gravity-dispersed tree that was trimmed regularly to prevent fruiting. Initial planting was between June and December 2006. Plots were replanted in September and October 2007

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after an extended seasonal drought killed the first cohorts (Martínez-Garza et al. 2011).

Eight exclosures were planted with 12 animal-dispersed species (four pioneer and eight

later-successional tree species); another eight exclosures were planted with 12 wind-

dispersed species (four pioneers and eight later-successional tree species; Table 3.7.1).

Eight unplanted exclosures served as controls. Each subplot was planted in a 6 × 6 grid,

with a total per plot of 144 plants (12 of each of 12 species) separated by 2 m from each

other (Figure 3.6.1). Twelve species in 16 planted plots were spaced to maximize distance

between conspecifics within each subplot. Growing vegetation within 50 cm of planted

seedlings was removed monthly until the sapling was taller than surrounding grass (to 1.5

m high). The matrix between fenced plots remained short, closely-cropped grass in active

pastures that were maintained as part of the experimental design. Cattle consumed

seedlings and kept grasses cropped up to a meter inside fences.

Plots differed in distance to forest. Plot midpoints were 90 - 480 m from 30 - 40 year-old

secondary forest (241 $\pm$ 18 m SE here and below) to the south and southeast of the grid,

and 236 - 409 m from privately-owned primary forest to the east (324 $\pm$ 12 m). Taller old-

growth forest of the Los Tuxtlas Biological Station was 344 - 800 m (568 $\pm$ 31 m) to the

south of plots.

Woody seedlings > 10 cm high, excluding planted individuals, were counted in each

fenced plot every four months from 20 through 60 months after cattle exclusion. Recruited

species were identified, tagged, measured (height and basal diameter, with diameter at

breast height and canopy width for growing trees). Re-sprouts of pre-existing trees (0 – 3

per plot) were cut. These were not counted in censuses. Nomenclature followed (Ibarra-

Manriquez and Sinaca 1995, Ibarra-Manriquez and Sinaca 1996a, b).

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3.2.3 Statistical analyses

The basic tool of the following analyses is repeated-measures ANOVA. We use a factorial design in which samples of recruits are measured on every four months, where the number of months since cattle exclusion is the repeated factor. Dependent variables are species recruitment rate for the first repeated-measures ANOVA, recruitment rate regardless of species for the second (hereafter "individual recruitment"). The repeated-measures ANOVAs included: 1) planting treatment with three levels (plots planted with animal-dispersed species, planted with wind-dispersed species, and unplanted controls); 2) life history with two levels (pioneer and later-successional recruits); and 3) dispersal mode with two levels (recruits from seeds dispersed by animals or wind). We evaluated overall significance levels for repeated measures using the Greenhouse-Geisser correction for sphericity. Means are accompanied by standard deviations unless otherwise indicated.

Statistical analyses were performed using STATISTICA 7.0 (StatSoft, Tulsa, OK, U.S.A.) and SYSTAT 13 (Chicago, IL., U.S.A). Derivative estimates and metrics addressing community structure (projected richness, alpha and beta diversities, multidimensional scaling, and similarity indices) will be developed elsewhere.

3.3 RESULTS

3.3.1 Overview

During 60 months of cattle exclosure, 44 woody species from 27 families recruited in a density of 0.057 individuals m^{-2} (Table 3.7.2). Overall survival of recruits was 81% after 60 months of cattle exclosure. Common families included Melastomataceae, Euphorbiaceae and Piperaceae, with 4, 4 and 3 species, respectively. *Bursera simaruba* (Burseraceae), a

later-successional animal-dispersed tree that is widely used as a shade tree and in living fences, had the highest density (0.017 individuals m^{-2}). *Cordia alliodora* (Boraginaceae), a pioneer species dispersed by wind, and *Conostegia xalapensis* (Melastomataceae), a pioneer animal-dispersed shrub were the second and third most important species by density (0.008 and 0.004 individuals m^{-2}, respectively). Fifty-six percent of the recruited seedlings were pioneers, 67% of which were of animal-dispersed taxa. The remaining 44% of the seedlings were later-successionals, of which 87% were animal-dispersed and 13% wind-dispersed.

Between 20 and 60 months since cattle exclusion, repeated-measures ANOVA indicated increases in recruitment of species and individuals. Species recruitment rate increased significantly over time in a roughly linear fashion ($F_{(10, 840)}$ = 51.11, P < 0.00001, Figure 3.6.2a). Individual recruitment also increased, with apparent acceleration between 44 and 60 months (repeated measures $F_{(10, 840)}$ = 21.72, P < 0.00001, Figure 3.6.2b). Of most interest were within-subject interactions of main effects with time.

3.3.2 Interactions with time

Interactions of time and response variables were evident. Interaction between time and planting treatments from 20 through 60 months showed significantly higher recruitment rates in planted versus control plots for species (repeated measures $F_{(20, 840)}$ = 2.54, *P* = 0.0002, Figure 3.6.3a) and individuals ($F_{(20, 840)}$ = 3.33, *P* < 0.0001, Figure 3.6.3b). Interaction of time and life-history showed a significantly higher increase of pioneer species recruitment rate as compared with later-successional species (repeated measures $F_{(10, 840)}$ = 11.43, *P* < 0.0001, Figure 3.6.4a). Individual recruitment rates did not differ by life histories ($F_{(10, 840)}$ = 0.95, *P* = 0.49, Figure 3.6.4b). Interaction of time and dispersal mode indicated a

larger increase in recruitment rates of animal-dispersed compared to wind-dispersed species (Figure 3.6.4c; repeated measures $F_{(10, 840)}$ = 7.44, P < 0.0001). Individual recruitment rates also differed between animal- and wind-dispersed trees and shrubs over time (Figure 3.6.4d; $F_{(10, 840)}$ = 1.84, P = 0.05).

Finely, interactions between treatments, life history, dispersal mode and time showed wide differences in individual recruitment rates (Figure 3.6.5; repeated measures $F_{(20, 840)}$ = 2.06, P = 0.004). Pioneer recruits did not differ among planting treatments (Figure 3.6.5a, 3.6.5b). Later-successional animal-dispersed recruits increased in planted plots, but not in controls (Figure 3.6.5c; $F_{(20,210)}$ = 3.09, P = 0.00002). Later successional wind-dispersed recruits did not change with planting treatments over time (Figure 3.6.5d). High recruitment rates of later-successional individuals of species dispersed by animals (Figure 3.6.5c) in plots of wind-dispersed trees was influenced by a precocious plot of greater soil depth (mean 42.5 cm) than other planted plots (21.5 ± 2.5 cm; log_{10} transformed to meet conditions of normality, t_{14} = - 7.3, P = 0.00001) that formed a closed canopy at 40 months. With this outlier excluded, recruitment in stands of wind- and animal-dispersed trees were indistinguishable Pooled planting treatments also differed from controls ($F_{(10,210)}$ = 3.68, P = 0.00015).

3.4 DISCUSSION

Restoration of tropical biodiversity in abandoned pastures requires recruitment of trees from surrounding forests and forest fragments. This is true whether abandoned land is released to natural secondary succession, whether monocultures of planted trees provide conditions necessary for establishment of shade-tolerant seedlings, or whether mixed-

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

3.4.1 Characterizing the recruited community

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

Challenges to restoration of biodiversity in abandoned pastures at Los Tuxtlas include seed and recruitment limitation of animal-dispersed trees from nearby forest remnants. Approximately 76% of rainforest tree species at Los Tuxtlas are dispersed by animals

(Ibarra- Manriquez and Oyama 1992). Over time one expects this majority of animal-dispersed taxa to increase because there are many more of them than wind-dispersed species. Biotically-dispersed seeds carried by wide-ranging bats or birds are more mobile than any but the smallest abiotically-dispersed seeds of primary-forest trees. Relevant issues for a given site are availability of seed sources of primary and old secondary forest, and how quickly rates of seed fall and particularly seedling recruitment change after pastures are abandoned.

Xeric pasture conditions and dispersal limitation pose serious impediments to restoration of tropical diversity on fallow land. High temperatures, direct solar radiation, low humidity, and little leaf litter preclude germination and establishment of many later-successional trees (Parrotta et al. 1997). Some of these do well in xeric pasture conditions if they are planted as seedlings (Martinez-Garza et al. 2005), but many do not establish from seed unless they arrive in scarce sites with enough shade and moisture to allow germination and establishment without competition from dense grasses (Otero-Arnáiz et al. 1999). Sixty months after cattle exclusion, ~15% of 300 local woody species are established in at least one of the three treatments. Low input of seeds and poor establishment of later-successional species explain this lag. Of most interest in our study, accelerating accumulation of animal-dispersed species of secondary and primary forest is evident in planted plots 48 months after cattle exclusion, but not in control plots. This likely reflects improving conditions for shade-tolerant seedlings arriving from forest 90-480 m away, and quite likely increasing attractiveness of planted plots to fruit-eating birds and mammals.

3.4.2 Recruitment in pastures and managed plantations

The effectiveness of seed dispersal from the plant perspective depends on where seeds

land (Schupp et al. 2010). Mature tree plantations in agricultural landscapes accelerate

seedling recruitment and ecological succession (Kuusipalo et al. 1995, Lugo 1997, Parrotta

et al. 1997, Powers et al. 1997, Keenan et al. 1999, Chazdon 2008). In general, recruitment of

woody plants into recently abandoned pastures is substantially lower than into

monospecific or mixed stands of planted trees that offer shade to seedlings and cover to

dispersal agents. In 15-16 year-old successional plots established on abandoned Costa

Rican pastures, for instance, natural recruitment of woody species is about half that into

monospecific stands of three species, or into mixed stands of the same three species

(Butler et al. 2008). Even with a clear general result, individual recruitment under some

monocultures overlaps with unplanted controls, indicating the need to further clarify

interactions between planted tree composition, dispersal, and recruitment.

Landscape features that attract animal dispersers into pastures play a critical role in

regeneration of tropical forest (Nepstad et al. 1996, Wunderle 1997, Martínez-Garza and

Howe 2003). For example, seed densities of heterospecifics in exclosures under isolated

remnant trees in pastures can be as high as in the understory of continuous forest (Slocum

2001, Laborde et al. 2008). Moreover, species matter. Seedling recruitment in enclosures

around isolated pasture trees is higher under sparse canopies, whether fruits are fleshy or

dry (Slocum 2001). Once cattle are excluded from pastures, remnant trees become

regeneration nuclei from which vegetation spreads (Holl et al. 2010). For pioneer trees, the

reproductive niche of large adults is often in vegetation too dense to allow establishment

of their own offspring, indicating an ontological niche shift between seedling and adult

requirements (see Miriti 2006). For instance, large *Miconia prasina* adults in Puerto Rico recruit far more seeds in open habitats than under their own canopies (Pascarella et al. 2007). Fenced plantings that attract fruit-eating animals potentially act as buffers around or stepping stones between forest remnants for recruitment of shade-tolerant seedlings, ultimately facilitating pollen and seed exchange among forest fragments and isolated tree stands.

In the present experiment, plots remained grass-covered for nearly a year following re-planting after a severe dry-season drought in 2007 killed most seedlings planted in 2006 (Martínez-Garza et al. 2011). Accordingly, cattle exclusion was the single most important factor contributing to increase of recruitment rates during the first 20 months, with substantial changes in soil and litter characteristics under a mantle of grass (Tobon et al. 2011, Roa-Fuentes et al. in press). At 20 months, eight since replanting, planted stands and recruits from natural dispersal grew without interruption.

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

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exclusion. Nonetheless, most individual seedling recruits (96%) were not of experimental

species. Of those that were, most individuals of *C. obtusifolia* established before planted

trees bore fruit. After 20 months, plantings provided resting sites, cover, and foraging

sites for birds that eat both insects and fruits, and eventually provided both fruit resources

for bats and birds that import seeds and environmental conditions that allowed shade-

tolerant colonists from nearby forests to establish.

3.4.3 Plant dynamics in an agricultural mosaic

Seeds must be present for recruitment to occur, but patterns of seedling recruitment often

do not closely reflect patterns of seed fall. At least 30 years of intense grazing pressure

have left Los Tuxtlas pastures with little litter over thin, eroded soils (Tobon et al. 2011).

In tropical soils few woody species other than pioneers are capable of long-term seed

dormancy (Dalling and Denslow 1997, Norden et al. 2009). Emerging seedlings from seed

banks at our Los Tuxtlas site are primarily those of animal-dispersed trees left as legacies

around stumps of figs (*Ficus* spp.) and *Bursera simaruba* that were cut during site

preparation (Howe et al. 2010). Virtually all recruits (96%) of trees during the first 60

months after cattle exclusion resulted from seed dispersal at least 90 – 480 m from seed

sources in forests or from isolated shade trees in pastures.

A simple distinction between animal- and wind-dispersed species gives insufficient

weight to complexities in both dispersal modes. Wind-dispersed species, ~ 24% of tree

species in the region, have a variety of dispersal strategies (see Wright et al. 2008). Initial

colonization in the Los Tuxtlas plots has been by long-distance dispersal of species with

small (< 0.05 g), widely-disseminated seeds of pioneers (e.g. *Cordia alliodora, Eupatorium

galeotti, Heliocarpus appendiculata, H. donnell-smithii*). Occasionally colonization of open

ground is dominated by later-successional wind-dispersed trees with small seeds (e.g. Tabebuia heterophylla in highland Puerto Rico; Zimmerman et al. 2000), but that is not the pattern at Los Tuxtlas. Aside from *Albizia purpusii*, a legacy species cut during site preparation (Howe et al. 2010), later-successional trees dispersed by wind are a negligible presence. We expect this dearth of recruitment of later-successional trees dispersed by wind to continue, other than by the eight species that we experimentally establish.

Animal behavior mediates dissemination of animal-dispersed plants. Forest birds and mammals differ in proclivity to cross open ground. Some move easily along edges, but hesitate to cross alien matrices (e.g. Levey et al. 2005); in the Los Tuxtlas landscape about 40% of 257 species of birds and mammals leave forest rarely, if at all (Estrada et al. 1993). Of the remaining 60%, many fruit-eating birds and bats live in the fragmented landscape and both distribute seeds of pioneers within the agricultural mosaic and bring seeds from forest trees into pastures (Guevara and Laborde 1993, Galindo-Gonzalez et al. 2000). Common visitors to our plots, including large bats (*Artibeus jamaicensis*) and birds (*Ramphastos sulfuratus*), travel hundreds of meters to preferred fruiting trees (Handley et al. 1991, Graham 2001). Such long-distance commuters are most likely to bring seeds of forest trees. In 60 months of cattle exclusion, recruitment of later-successional trees shows no sign of an asymptote; quite the contrary, species recruitment is increasing and individual recruitment is accelerating.

Recruitment patterns underscore differences among ecosystems. In early secondary growth in temperate South Carolina, richness of wind-dispersed plants increases over seven years, while animal-dispersed species asymptote in five years (Damschen et al. 2008). In our study of tropical trees, dispersal limitation of later-successional trees

dispersed by wind is the rule, excepting trees that we plant (Martínez-Garza and González-Montagut 1999, Martínez-Garza et al. 2009). At Los Tuxtlas, with ~ 100 species of fruit-eating birds and mammals and 230 species of animal-dispersed trees of old secondary and primary forest, recruitment of new species into experimental plots will continue to increase until priority effects of shade-tolerant saplings and adults suppresses newcomers (Hubbell et al. 1999). The present the rate of recruitment of later-successional animal-dispersed tree seedlings remains < one in 100 m^{-2} month^{-1}, with no sign of leveling off.

3.4.4 Future composition

Stands of trees in agricultural mosaics have the potential to increase or maintain diversity of animal-dispersed plants and fruit-eating animals that would otherwise be lost. Such habitat patches additionally may provide pollen and seed exchange among forest remnants (see Turner and T. Corlett 1996, Graham 2001, Hughes et al. 2002, Kramer et al. 2008). Seeds of forest trees species will arrive, carried by birds and bats that commute from forest to feeding sites. The flora and fauna of small habitat patches will be subsets of those in continuous forest (Cordeiro et al. 2009), but at Los Tuxtlas they will be large subsets (Estrada et al. 1993). Effective dispersal agents of seeds of forest trees into synthetic plant communities will be commuters from forest that fly substantial distances to and from habitat patches in which they forage, and they already appear to be bringing seeds of species that do not arrive in grassy control plots.

A caveat is that the future patterns of seed or seedling mortality within synthetic habitat patches are not yet knowable. There is no indication of density-dependent mortality among conspecific immigrant seedlings, nor is there yet evidence of density-dependent

mortality across species from generalized seed or seedling predators (Kwit et al. 2004). To date seedling densities remain low, and what mortality occurs is likely density-independent. As planted trees begin to produce large fruit crops, negative density-dependent mortality of seeds and seedlings is certain to increase (Harms et al. 2000, Alvarez-Loayza and Terborgh 2011). The much larger pool of forest tree species likely to colonize our plots relative to planted species is likely to increase recruitment success well before density-dependence occurs. Under this scenario we expect species accumulation to increase in stands of animal-dispersed trees that serve as magnets for bird and bat dispersal agents more than in stands of wind-dispersed trees that offer little food.

3.4.5 Conclusion

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

Conversely, it is useful to ask where assisted succession is a good idea (Holl and Aide 2011). Abandoned land on deep soils near forest seed sources may well recover quickly without assistance if dispersal agents are common in the landscape. If land is abandoned or may be acquired on such sites, unassisted succession may be cost-effective. A different solution applies to land perceived as too valuable to abandon, which is the case at Los Tuxtlas. In permanent agricultural mosaics, stepping-stone forest patches could serve an

important function in maintaining "countryside diversity" of both plants and animals (Turner and T. Corlett 1996, Daily et al. 2001, Hughes et al. 2002), while preserving a degree of connectivity during a period of historically rapid climate change (Corlett 2011). On our site unassisted succession is slow; planted trees that grow rapidly are likely to increase recruitment of animal-dispersed trees of old secondary and primary forest, ultimately providing stands of young adult trees of many species that provide food for fruit-eating animals, mates through long-distance pollination for widely dispersed "populations" of trees (Kramer et al. 2008), and seed exchange among small forest fragments and larger remnants. Stepping-stone patches, more widely spaced than our experimental design permits, may serve a critical purpose in maintaining connectivity among forest fragments and maintaining biodiversity in highly altered landscapes.

3.5 LITERATURE CITED

Aide, T. M., J. K. Zimmerman, L. Herrera, M. Rosario, and M. Serrano. 1995. Forest recovery in abandoned tropical pastures in Puerto-Rico. Forest Ecology and Management 77:77-86.

Alvarez-Loayza, P., and J. Terborgh. 2011. Fates of seedling carpets in an Amazonian floodplain forest: intra-cohort competition or attack by enemies? Journal of Ecology 99:1045-1054.

Benítez-Malvido, J., and A. Lemus-Albor. 2005. The Seedling Community of Tropical Rain Forest Edges and Its Interaction with Herbivores and Pathogens[1]. Biotropica 37:301-313.

Bohrer, G., G. G. Katul, R. Nathan, R. L. Walko, and R. Avissar. 2008. Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. Journal of Ecology 96:569-580.

Bryant, D., D. Nielsen, and L. Tangley. 1997. The last frontier forests: ecosystems and economies on the edge.*in* W. r. institute, editor., Washington, d.c.

Butler, R., F. Montagnini, and P. Arroyo. 2008. Woody understory plant diversity in pure and mixed native tree plantations at La Selva Biological Station, Costa Rica. Forest Ecology and Management 255:2251-2263.

Cordeiro, N. J., H. J. Ndangalasi, J. P. McEntee, and H. F. Howe. 2009. Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. Ecology 90:1030-1041.

Corlett, R. T. 2011. Impacts of warming on tropical lowland rainforests. Trends in ecology & evolution (Personal edition) 26:606-613.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6:51-71.

Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science 320:1458-1460.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica. Ecological Applications 11:1-13.

Dalling, J. W., and J. S. Denslow. 1997. Soil seed bank composition along a forest chronosequence in seasonally moist tropical forest, Panama. Journal of Vegetation Science 9:669-678.

Damschen, E. I., L. A. Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, and J. J. Tewksbury. 2008. The movement ecology and dynamics of plant communities in fragmented landscapes. Proceedings of the National Academy of Sciences 105:19078-19083.

Dirzo, R. 2001. Tropical forests. Pages 251-276 *in* O. Sala, F. S. Chapin, and E. Huber-Sannwald, editors. Global Biodiversity in a Changing Environment. Springer-Verlag, Nueva York.

Dirzo, R., E. González Soriano, and Vogt C. R. 1997. La región de Los Tuxtlas: introducción general. Pages 3-6 *in* E. González-Soriano, R. Dirzo, and R. C. Vogt, editors. Historia natural de Los Tuxtlas. Uiversidad Nacional Autónoma de México, Instituto de Biología, México, D.F.

Estrada, A., and R. Coates-Estrada. 2001. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. Pages 627-646. Cambridge Journals Online.

Estrada, A., and R. Coates-Estrada. 2005. Diversity of Neotropical migratory landbird species assemblages in forest fragments and man-made vegetation in Los Tuxtlas, Mexico. Biodiversity and Conservation 14:1719-1734 (1716).

Estrada, A., R. Coates-Estrada, and D. Meritt. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16:309-318.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Fearnside, P. M. 1999. Can pasture intensification discourage deforestation in the Amazon and pantanal regions of Brazil?*in* Patterns and Processes of Land-Use and Forest Change. 23-26 March, University of Florida, Gainesville, Florida.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881-919.

Galindo-Gonzalez, J., S. Guevara, and V. J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14:1693-1703.

Graham, C. H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology 15:1789-1798.

Guevara, S., L. J., and G. Sánchez-Ríos. 2004. Los Tuxtlas. El paisaje de la sierra. Instituto de Ecología, A.C. - Unión Europea, Xalapa, Ver.

Guevara, S., and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio 107/108:319-338.

Handley, C. O., A. L. Gardner, and D. E. Wilson. 1991. Movements, demography and natural history of the common fruit bat, Artibeus jamaicensis, on Barro Colorado Island, Panama. Smithsonian Institution Press, Washington.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493-495.

Holl, K. D., and T. M. Aide. 2011. When and where to actively restore ecosystems? Forest Ecology and Management 261:1558-1563.

Houghton, R. A. 1994. The worldwide extent of land-use change. Bioscience 44:305-313.

Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539-550.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Howe, H. F., Y. Urincho-Pantaleon, M. de la Peña-Domene, and C. Martinez-Garza. 2010. Early seed fall and seedling emergence: precursors to tropical restoration. Oecologia 164:731-740.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. L. de Lao. 1999. Light-Gap Disturbances, Recruitment Limitation, and Tree Diversity in a Neotropical Forest. Science 283:554-557.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 2002. Conservation of tropical forest birds in countryside habitats. Ecology Letters 5:121-129.

Ibarra- Manriquez, G., and K. Oyama. 1992. Ecological correlates of reproductive traits of Mexican rain-forest trees. American Journal of Botany 79:383-394.

Ibarra-Manriquez, G., and S. Sinaca. 1995. Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México. . Revista De Biologia Tropical 43:75-115.

Ibarra-Manriquez, G., and S. Sinaca. 1996a. Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Mimosaceae a Verbenaceae). Revista De Biologia Tropical 44:41-60.

Ibarra-Manriquez, G., and S. Sinaca. 1996b. Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Violaceae a Zingiberaceae). Revista De Biologia Tropical 44:427-447.

Ingle, N. R. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. Oecologia 134:251-261.

Janzen, D. H. 1988. Management of habitat fragments in a tropical dry forest - growth. Annals of the Missouri Botanical Garden 75:105-116.

Jones, F. A., C. J. Peterson, and B. L. Haines. 2003. Seed predation in neotropical pre-montane pastures: site, distance, and species effects. Biotropica 35:219-225.

Keenan, R. J., D. Lamb, J. Parrotta, and J. Kikkawa. 1999. Ecosystem management in tropical timber plantations: satisfying economic, conservation, and social objectives. Journal of Sustainable Forestry 9:117 - 134.

Kramer, A. T., J. L. Ison, M. V. Ashley, and H. H. F. 2008. The Paradox of Forest Fragmentation Genetics. Conservation Biology 22:878 - 885.

Kuusipalo, J., G. Ådjers, Y. Jafarsidik, A. Otsamo, K. Tuomela, and R. Vuokko. 1995. Restoration of natural vegetation in degraded *Imperata cylindrica* grassland: understorey development in forest plantations. Journal of Vegetation Science 6:205-210.

Kwit, C., D. J. Levey, and C. H. Greenberg. 2004. Contagious seed dispersal beneath heterospecific fruiting trees and its consequences. Oikos 107:303-308.

Laborde, J., S. Guevara, and G. Sanchez-Rios. 2008. Tree and shrub seed dispersal in pastures: The importance of rainforest trees outside forest fragments. EcoScience 15:6-16.

Levey, D. J., B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad. 2005. Effects of Landscape Corridors on Seed Dispersal by Birds. Science 309:146-148.

Lugo, A. E. 1997. The apparent paradox of reestablishing species richness on degraded lands with tree monocultures. Forest Ecology and Management 99:9-19.

Martínez-Garza, C., A. Flores-Palacios, M. De La Peña-Domene, and H. F. Howe. 2009. Seed rain in a tropical agricultural landscape. Journal of Tropical Ecology 25:541-550.

Martínez-Garza, C., and R. González-Montagut. 1999. Seed rain from forest fragments into tropical pastures in Los Tuxtlas, Mexico. Plant Ecology 145:255-265.

Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. Journal of Applied Ecology 40:423-429.

Martinez-Garza, C., V. Pena, M. Ricker, A. Campos, and H. F. Howe. 2005. Restoring tropical biodiversity: Leaf traits predict growth and survival of late-successional trees in early-successional environments. Forest Ecology and Management 217:365-379.

Martínez-Garza, C., W. Tobon, J. Campo, and H. F. Howe. 2011. Drought mortality of tree seedlings in an eroded tropical pasture. Land Degradation & Development:n/a-n/a.

Miriti, M. N. 2006. Ontogenetic shift from facilitation to competition in a desert shrub. Journal of Ecology 94:973-979.

Myster, R. W. 2004. Post-agricultural invasion, establishment, and growth of neotropical trees. Botanical Review 70:381-402.

Nepstad, D. C., C. Uhl, C. A. Pereira, and J. M. C. daSilva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos 76:25-39.

Nepstad, D. C., C. Uhl, and E. A. S. Serrao. 1991. Recuperation of a Degraded Amazonian Landscape - Forest Recovery and Agricultural Restoration. Ambio 20:248-255.

Norden, N., M. I. Daws, C. Antoine, M. A. Gonzalez, N. C. Garwood, and J. Chave. 2009. The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. Functional Ecology 23:203-210.

Ojima, D. S., K. A. Galvin, and B. L. Turner. 1994. The Global Impact of Land-Use Change. Bioscience 44:300-304.

Otero-Arnáiz, A., S. Castillo, J. Meave, and G. Ibarra-Manriquez. 1999. Isolated pasture trees and the vegetation under their canopies in the Chiapas Coastal Plain, Mexico. Biotropica 31:243-254.

Parrotta, J. A., J. W. Turnbull, and N. Jones. 1997. Catalyzing native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:1-7.

Pascarella, J., T. Aide, and J. K. Zimmerman. 2007. The Demography of Miconia prasina (Melastomataceae) During Secondary Succession in Puerto Rico. Biotropica. 39:54-61.

Powers, J. S., J. P. Haggar, and R. F. Fisher. 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. Forest Ecology and Management 99:43-54.

Rudel, T. K., O. T. Coomes, E. Moran, F. Achard, A. Angelsen, J. C. Xu, and E. Lambin. 2005. Forest transitions: towards a global understanding of land use change. Global Environmental Change-Human and Policy Dimensions 15:23-31.

Schupp, E. W., P. Jordano, and J. M. Gomez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333-353.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology 82:2547-2559.

Tobon, W., C. Martinez-Garza, and J. Campo. 2011. Soil responses to restoration of a tropical pasture in Veracruz, south-eastern Mexico. Journal of Tropical Forest Science 23:338-344.

Turner, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. Journal of Applied Ecology 33:200-209.

Turner, I. M., and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology & Evolution 11:330-333.

Uhl, C., R. Buschbacher, and E. A. S. Serrão. 1988. Abandoned pastures in eastern Amazonia: patterns of plant succession. Journal of Ecology 76:663.

Wright, S. J. 2010. The future of tropical forests. Annals of the New York Academy of Sciences 1195:1-27.

Wright, S. J., A. Trakhtenbrot, G. Bohrer, M. Detto, G. G. Katul, N. Horvitz, H. C. Muller-Landau, F. A. Jones, and R. Nathan. 2008. Understanding strategies for seed dispersal by wind under contrasting atmospheric conditions. Proceedings of the National Academy of Sciences 105:19084-19089.

Wunderle, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223-235.

Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology 8:350-360.

3.6 FIGURES
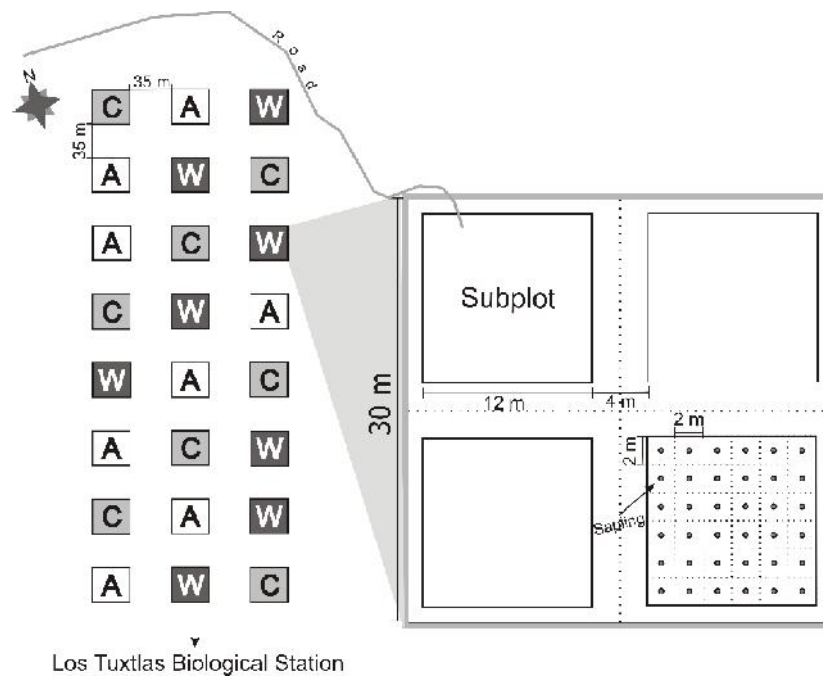
Figure 3.6.1 Experimental design of fenced plots. Illustrated are plantings of 12 animal-dispersed species (A), 12 wind-dispersed species (W), and unplanted controls (C).
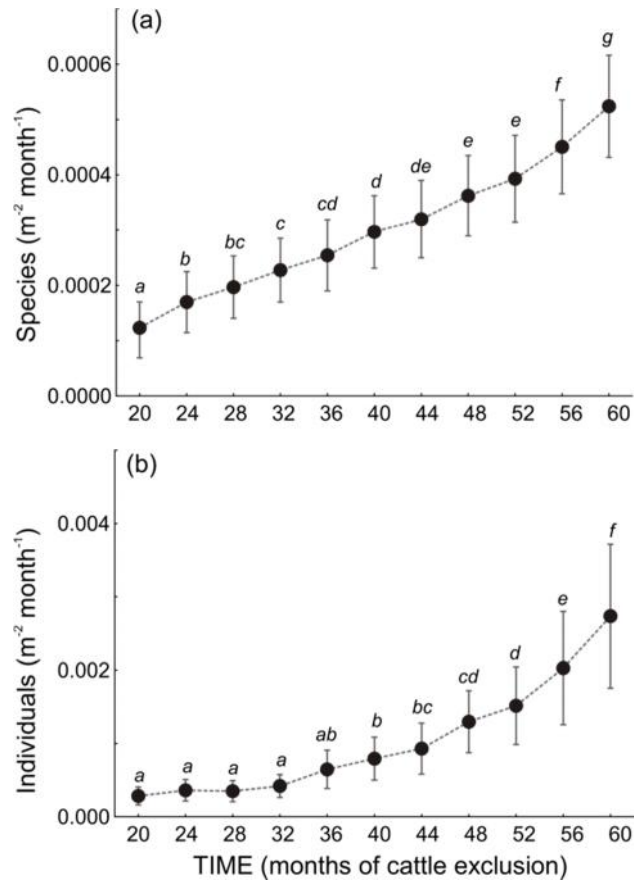
Figure 3.6.2 Species and individual recruitment rates through 60 months of cattle exclusion (through June 2011) for (a) species and (b) individuals. Shown are means with 95% confidence intervals. Note differences in scales of y – axes. Different letters indicate significant differences between time periods based on post-hoc Tukey tests at $P < 0.05$. See text for statistics.
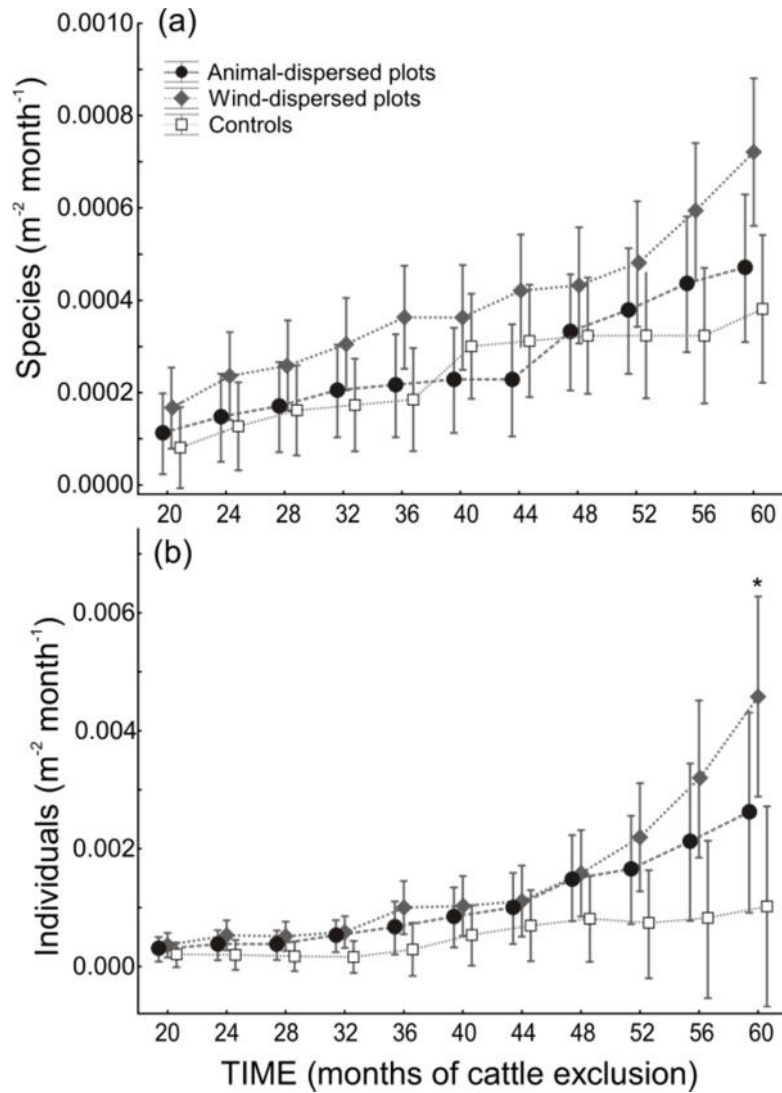
Figure 3.6.3 Species and individual recruitment rates by planting treatment. Means are represented by diamonds (controls), squares (wind-dispersed plantings) and circles (animal-dispersed plantings). Error bars indicate 95% confidence intervals. Wind-dispersed plots show higher individual recruitment rate than controls: Tukey test, * P < 0.05. See text for statistics.
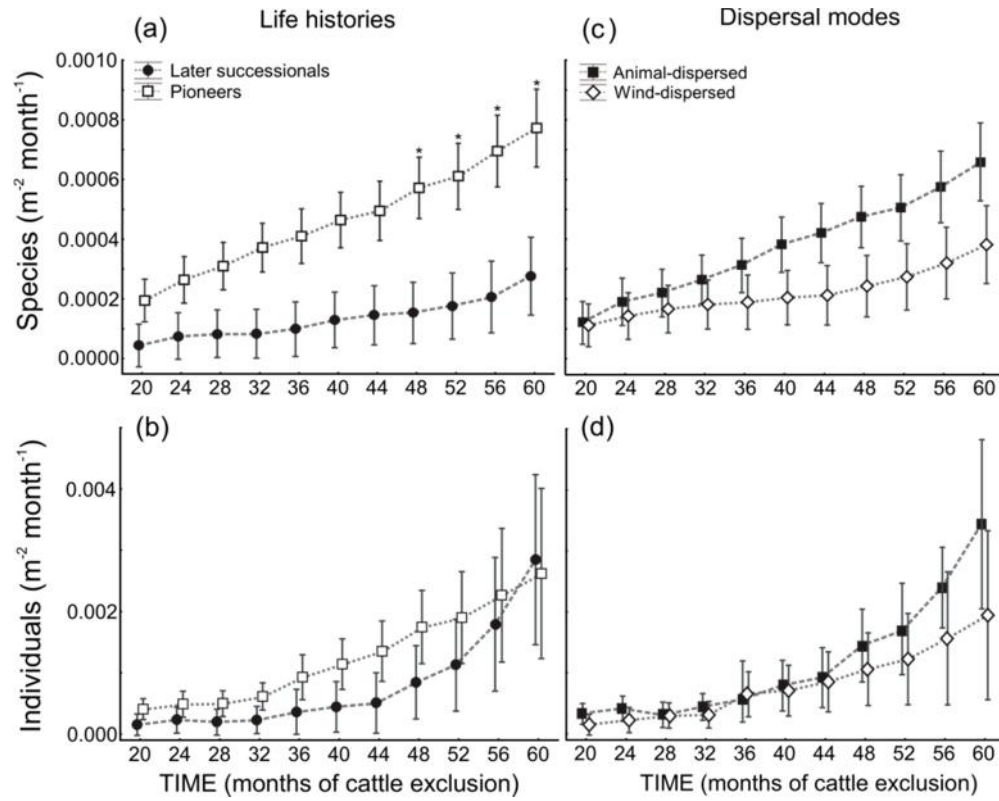
Figure 3.6.4 Species recruitment and individual recruitment rates for tree seedlings of pioneer and later-successional species (a, b) and animal- or wind-dispersed species (c, d). Error bars indicate 95% confidence intervals. See text for statistics.
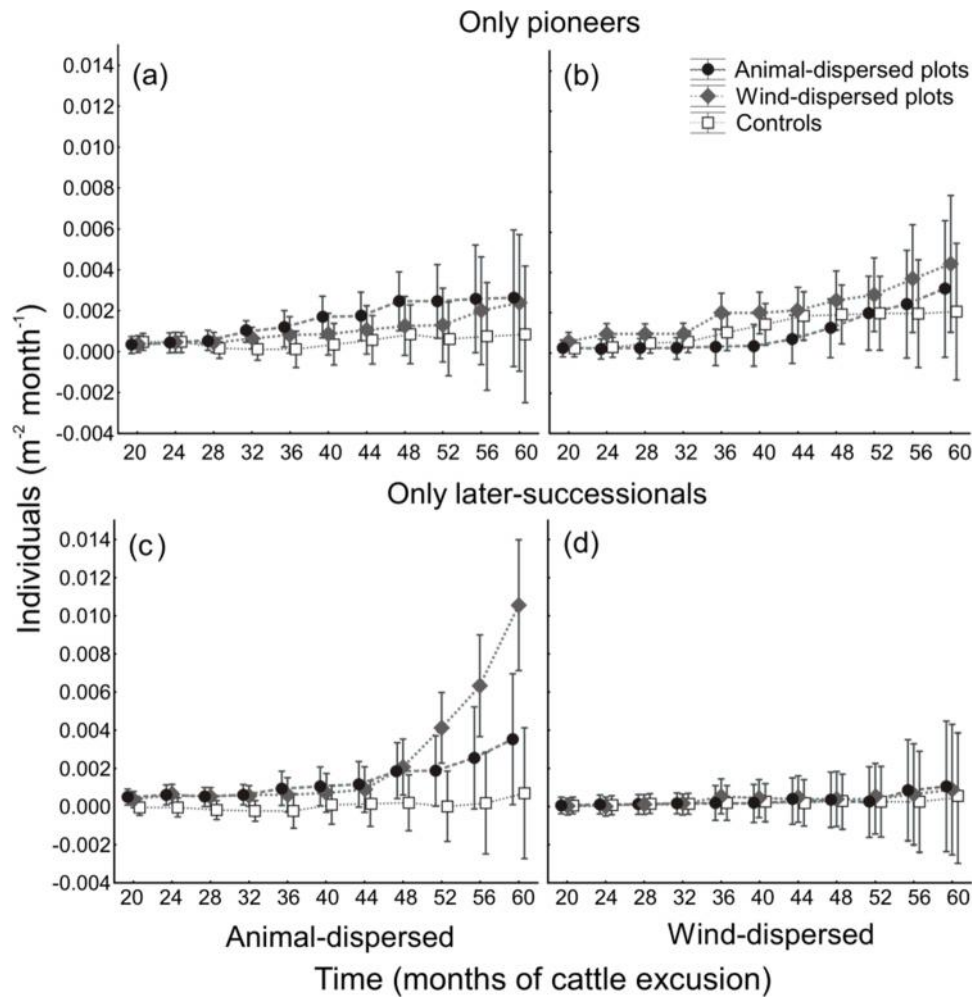
Figure 3.6.5 Individual recruitment rates of pioneer and later-successional trees and shrubs in three planting treatments. Means are represented by circles (animal-dispersed plantings), squares (wind-dispersed plantings), and diamonds (control plots). Error bars indicate 95% confidence intervals. See text for statistics.

3.7 APPENDICES

Table 3.7.1. Selection of planted species. Family, life history (pioneer or later-successional), and dispersal mode of species planted in 16 experimental plots at Los Tuxtlas, Veracruz, México. Sizes as of June 2011 are presented as means ± sd. Nomenclature follows Ibarra-Manríquez & Sinaca (1995, 1996, 1996a, b). Life-history classification is based on Martinez-Ramos (1985).

| *Species*	*Family*	*Life strategy*	*Height (cm)*	*Dbh (mm)*	*Canopy (cm2)*
Animal-dispersed species					
Cecropia obtusifolia	Cecropiaceae	Pioneer	557 ± 196	84 ± 30	50,623 ± 48,440
Ficus yoponensis.	Moraceae	Pioneer	280 ± 112	44 ± 37	51,640 ± 61,655
Rollinia jimenezii	Annonaceae	Pioneer	189 ± 113	21 ± 13	2,527 ± 5,814
Stemmadenia donnell-smithii	Apocynacaea	Pioneer	155 ± 67	21 ± 23	8,520 ± 11,659
Amphitecna tuxtlensis	Bignoniaceae	Late	133 ± 64	33 ± 34	1,712 ± 5,896
Brosimum alicastrum	Moraceae	Late	145 ± 112	29 ± 31	1,111 ± 8,236
Cojoba arborea	Mimosaceae	Late	240 ± 76	32 ±14	31,388 ± 39,257
Dussia mexicana	Fabaceae	Late	132 ± 40	21 ± 9	681 ± 2,056
Guarea glabra	Meliaceae	Late	126 ± 55	41 ± 35	1,035 ± 6,399
Inga sinacae	Mimosaceae	Late	258 ± 78	28 ± 18	34,918 ± 48,378
Poulsenia armata	Moraceae	Late	119 ± 56	31 ± 26	1,894 ± 5,703
Pouteria sapota	Sapotaceae	Late	114 ± 66	32 ± 8	946 ± 2,235
Wind-dispersed species					
Cedrela odorata	Meliaceae	Pioneer	235 ± 106	27 ± 15	15,679 ± 27,097
Ceiba pentandra	Bombacaceae	Pioneer	173 ± 86	25 ± 12	5,113 ± 8,080
Heliocarpus appendiculata	Tiliaceae	Pioneer	229 ± 65	37 ± 18	16,314 ± 18,612
Ochroma pyramidale	Bombacaceae	Pioneer	434 ± 160	85 ± 37	154,797 ± 143,665
Albizia purpusii	Mimosaceae	Late	421 ± 217	77 ± 45	27,066 ± 76,512
Aspidosperma megalocarpon	Apocynacaea	Late	144 ± 54	15 ± 14	2,730 ± 10,619
Bernoullia flammea	Bombacaceae	Late	128 ± 87	34 ± 19	2,027 ± 4,766
Cordia megalantha	Boraginaceae	Late	84 ± 52	15 ± 6	1,336 ± 5,067
Lonchocarpus guatemalensis	Fabaceae	Late	233 ± 113	32 ± 19	8,361 ± 23,930
Platymiscium pinnatum	Fabaceae	Late	301 ±157	38 ± 20	26,008 ± 40,904
Tabebuia guayacan	Bignoniaceae	Late	165 ± 85	21 ± 12	4,593 ± 10,417
Vochysia guatemalensis	Vochysiaceae	Late	231 ± 67	31 ± 16	16,807 ± 25,592

Ibarra-Manríquez, G., and S. Sinaca-Colín. 1996. Annotated checklist of plants from "Los Tuxtlas" Biological Station, Veracruz, Mexico: (Violaceae-Zingiberaceae). Revista De Biologia Tropical 44:427-447.

Ibarra-Manriquez, G., and S. Sinaca. 1995. Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México. . Revista De Biologia Tropical 43:75-115.

Ibarra-Manriquez, G., and S. Sinaca. 1996a. Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Mimosaceae a Verbenaceae). Revista De Biologia Tropical 44:41-60.

Ibarra-Manriquez, G., and S. Sinaca. 1996b. Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Violaceae a Zingiberaceae). Revista De Biologia Tropical 44:427-447.

Martínez-Ramos, M. 1985. Claros, ciclos vitales de los árboles tropicales y la regeneración natural de las selvas altas perennifolias. Pages 191-239 *in* A. G.-P. S. d. Amo, editor. Investigaciones sobre la Regeneración de las Selvas Altas en Veracruz, México Editorial Alhambra Mexicana, S.A., México, D.F.

Table 3.7.2 Recruited species in agricultural pasture of Los Tuxtlas, Mexico after 60 months of cattle exclosure. General information on life strategy and dispersal mode are presented for each species based on published information, total number of recruited individuals and percentage of survival. Increments in height are calculated as means and standard deviations of final measurement (June 2011) of all individuals of each species. Botanical nomenclature follows Ibarra-Manriquez 1995-1996. Means are accompanied by one standard deviation.

Species	Family	Successional status	Life Form	Dispersal mode	Total (N)	Surv. (%)	Height (cm)	DBH (mm)	Canopy cover (cm²)
Acacia cornígera	Mimosaceae	Pioneer[1,2,3]	Tree	animal	9	89	125 ± 123	26 ± 35	10,394 ± 21,992
Albizia purpusii	Mimosaceae	Late[3,4]	Tree	wind	57	91	208 ± 144	61 ± 132	18,072 ± 36,498
Alchornea latifolia	Euphorbiaceae	Late[1,3]	Tree	animal	8	88	165 ± 200	20 ± 22	6,499 ± 9,859
Bursera simaruba	Burseraceae	Late[1,5]	Tree	animal	337	89	119 ± 130	21 ± 25	7,759 ± 18,091
Cecropia obtusifolia	Cecropiaceae	Pioneer[1,2,3,6]	Tree	animal	36	89	603 ± 343	47 ± 34	119,376 ± 129,125
Cedrela odorata.	Meliaceae	Pioneer[7]	Tree	wind	13	92	124 ± 102	35 ± 33	8,515 ± 14,107
Ceiba pentandra	Malvaceae	Pioneer[7]	Tree	wind	1	100			
Cestrum racemosum	Solanaceae	Pioneer[5,6]	Tree	animal	6	83	250 ± 87	64 ± 41	22,423 ± 18,434
Clidemia sp.	Melastomataceae	Pioneer[2]	Shrub	animal	12	58	127 ± 26	27 ± 14	4,947 ± 3,270
Clusia sp.	Clusiaceae	Late[4]	Tree	animal	5	60	117 ± 16	20 ± 8	3,736 ± 2,014
Cnidoscolus multilobus	Euphorbiaceae	Pioneer[1,5,6]	Tree	wind	3	100	150 ± 229	42 ± 68	18,507 ± 31,721
Coccoloba hondurensis	Polygonaceae	Late[1]	Tree	animal	3	100	293	27	7,396 ± 10,200
Conostegia xalapensis	Melastomataceae	Pioneer[1,2,3]	Shrub	animal	54	81	189 ± 81	46 ± 26	28,255 ± 22,611
Cordia alliodora	Boraginaceae	Pioneer[3,7]	Tree	wind	121	86	146 ± 138	22 ± 20	10,374 ± 17,766
Cupania glabra	Sapindaceae	Late[1,3]	Tree	animal	5	80	368 ± 243	44 ± 25	14,788 ± 12,848
Cymbopetalum baillonii	Annonaceae	Late[1,3,5]	Tree	animal	1	100	30	6	657
Dalbergia glomerata	Fabaceae	Late[1,3]	Tree	wind	2	50	292	101	42,883
Eupatorium galeotii	Asteraceae	Pioneer[5]	Tree	wind	53	94	212 ± 141	51 ± 60	35,050 ± 50,300
Ficus aurea	Moraceae	Late[5]	Tree	animal	1	100	150	30	4,841

Species	Family	Successional status	Life Form	Dispersal mode	Total (N)	Surv. (%)	Height (cm)	DBH (mm)	Canopy cover (cm²)
Gliricidia sepium	Fabaceae	Pioneer [Introduced, 8]	Tree	wind	2	100	291 ± 153	38 ± 26	16,401 ± 16,791
Hampea nutricia	Malvaceae	Pioneer [1,3,5,6]	Tree	animal	7	100	173 ± 240	11 ± 9	21,377 ± 39,350
Heliocarpus appendiculatus	Tiliaceae	Pioneer [1,3,5,6]	Tree	wind	23	91	534 ± 235	149 ± 237	175,241 ± 162,408
Heliocarpus donnell-smithii	Tiliaceae	Pioneer [1,3,5,6]	Tree	wind	19	95	309 ± 209	40 ± 30	80,075 ± 118,132
Lippia macrophylla	Verbenaceae	Pioneer [2]	Shrub	animal	5	100	316 ± 91	50 ± 52	30,996 ± 26,496
Mangifera indica	Anacardiaceae	Late [Introduced, 9]	Tree	animal	3	100	143 ± 13	29 ± 2	3,461 ± 419
Miconia sp.	Melastomataceae	Pioneer [7,10]	Either	animal	3	67	113	23	3,770
Ochroma pyramidale	Bombacaceae	Pioneer [1,5,6]	Tree	wind	1	0			
Ocotea uxpanapana	Lauraceae	Late [1,5]	Tree	animal	2	100	25	4	24
Piper amalago	Piperaceae	Pioneer [3,4,5]	Tree	animal	9	78	153 ± 134	23 ± 32	13,495 ± 15,095
Piper hispidum	Piperaceae	Pioneer [1,2,5]	Shrub	animal	7	43			
Piper sp.	Piperaceae	Pioneer [1,2,5,6]	Either	animal	6	67			
Piper umbellatum	Piperaceae	Pioneer [2,6]	Shrub	animal	18	50	176 ± 90	20 ± 15	17,883 ± 15,420
Pleuranthodendron lindenii	Salicaceae	Pioneer [2,6]	Tree	animal	12	100	47 ± 18	6 ± 2	901 ± 646
Pseudolmedia oxyphyllaria	Moraceae	Late [2,7]	Tree	animal	1	100	22	5	471
Psidium guajava	Myrtaceae	Pioneer [1,4,5]	Tree	animal	8	88	168 ± 59	23 ± 4	8,777 ± 7,081
Phsycotria limonensis	Rubiaceae	Late [11,12]	Shrub	animal	3	100	77 ± 13	11 ± 6	3,963 ± 4,272
Rollinia jimenezii	Annonaceae	Late [3]	Tree	animal	1	100	400	71	84,383
Sapindus saponaria	Sapindaceae	Late [1]	Tree	animal	13	77	246 ± 139	42 ± 27	12,431 ± 14,075
Sapium nitidum	Euphorbiaceae	Pioneer [1,2]	Tree	animal	2	100	243 ± 306		46,851 ± 65,919
Stemmadenia donnell-smithii	Apocynaceae	Pioneer [3,5,6]	Tree	animal	2	100	170 ± 162	43 ± 54	16,284 ± 22,133
Tabernaemontana alba	Apocynaceae	Late [7]	Tree	animal	10	100	112 ± 91	21 ± 26	7,087 ± 17,169
Tetrorchidium rotundatum	Euphorbiaceae	Late [1]	Tree	animal	27	44	311 ± 223	50 ± 28	44,843 ± 61,740

Species	Family	Successional status	Life Form	Dispersal mode	Total (N)	Surv. (%)	Height (cm)	DBH (mm)	Canopy cover (cm²)
Trema micrantha	Ulmaceae	Pioneer [1,3,5,6]	Tree	animal	16	100	414 ± 187	67 ± 26	133,421 ± 166,990
Trophis mexicana	Moraceae	Late [1,3,4,5]	Tree	animal	1	100			
Verbesina crocata	Asteraceae	Pioneer [13]	Shrub	wind	2	100	325 ± 49	40	39,221 ± 28,254
Witheringia nelsonii	Solanaceae	Pioneer [6,10]	Shrub	animal	29	69	117 ± 76	22 ± 14	7,022 ± 14,950
Unknown	Verbenaceae		?		1	100			
					960	86			

References

1. Ibarra-Manriquez, G., M.M. Ramos, and K. Oyama, *Seedling functional types in a lowland rain forest in Mexico.* American Journal of Botany, 2001. 88(10): p. 1801-1812.

2. Purata, S., *Transect analysis a basis for comparing of old-field succession in a tropical rain forest area in Mexico.* Tropical Ecology, 1986. 27: p. 103-122.

3. Ibarra- Manriquez, G. and K. Oyama, *Ecological correlates of reproductive traits of Mexican rain-forest trees.* American Journal of Botany, 1992. 79(4): p. 383-394.

4. Bongers, F., et al., *Structure and Floristic Composition of the Lowland Rain-Forest of Los-Tuxtlas, Mexico.* Vegetatio, 1988. 74(1): p. 55-80.

5. Martínez-Ramos, M., *Claros, ciclos vitales de los árboles tropicales y la regeneración natural de las selvas altas perennifolias*, in *Investigaciones sobre la Regeneración de las Selvas Altas en Veracruz, México* A.G.-P.S.d. Amo, Editor 1985, Editorial Alhambra Mexicana, S.A.: México, D.F. p. 191-239.

6. Popma, J., F. Bongers, and M.J.A. Werger, *Gap-dependance and leaf characteristics of trees in a tropical lowland rain-forest in Mexico.* Oikos, 1992. 63(2): p. 207-214.

7. Comita, L.S., et al., *Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest.* Journal of Vegetation Science, 2007. 18(2): p. 163-174.

8. Anoka, U.A., I.O. Akobundu, and S.N.C. Okonkwo, *Effects of Gliricidia sepium (Jacq.) Steud and Leucaena leucocephala (Lam.) de Wit on growth and development of Imperata cylindrica (L.) Raeuschel.* Agroforestry Systems, 1991. 16(1): p. 1-12.

9. Arroyo-Rodríguez, V., et al., *Angiosperms, Los Tuxtlas Biosphere Reserve, Veracruz, Mexico.* Check List, Campinas, 2009. 5(4): p. 787-799.

10. Butler, R., F. Montagnini, and P. Arroyo, *Woody understory plant diversity in pure and mixed native tree plantations at La Selva Biological Station, Costa Rica.* Forest Ecology and Management, 2008. 255(7): p. 2251-2263.

11. Aide, T.M., et al., *Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology.* Restoration Ecology, 2000. 8(4): p. 328-338.

12. Berens, D.G., et al., *Exotic guavas are foci of forest regeneration in Kenyan farmland.* Biotropica, 2008. 40(1): p. 104-112.

13. Ibarra-Manriquez, G. and S. Sinaca, *Lista floristica comentada de la Estación de Biología Tropical "Los Tuxtlas", Veracruz, México (Mimosaceae a Verbenaceae).* Revista de Biología Tropical, 1996. 44: p. 41-60.

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CHAPTER IV

4. ROLES OF BIRDS AND BATS IN EARLY TROPICAL-FOREST RESTORATION

Roles of Birds and Bats in Early Tropical-Forest Restoration

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4.1 INTRODUCTION

The future of tropical forests will be determined by interplay of climate change,

conservation, deforestation, natural succession, and ecological restoration (Lamb et al.

2005, Chazdon 2008, Corlett 2011). Seed dispersal by birds and mammals plays a key role

in tropical forest dynamics, and will play a critical role in determining which tree species

migrate or vanish in response to changes in land use and climate (Corlett 2011). Fruit-

eating animals that regurgitate, defecate or bury seeds in viable condition are responsible

for effective reproduction of most tropical trees (Howe 1986, Wang and Smith 2002,

Muller-Landau and Hardesty 2005). One unaddressed challenge is to determine the roles

that different dispersal agents play in restoration of dispersal processes, which is the issue

at hand here (Wunderle 1997, Galindo-Gonzalez et al. 2000). A second challenge is to

harness those dispersal agents that most accelerate the process (Martínez-Garza and Howe

2003). We address the first challenge and offer a solution to the second for the first 76

months of succession in an agricultural mosaic of pasture, forest remnants, living fences

and scattered shade trees with a substantial residual fauna of fruit-eating birds and bats.

Here we address ecological results and consequences of dispersal processes that are

relevant to maintaining heterogeneity and accelerating ecological succession in highly

altered agricultural landscapes. Our approach uses the interdependence of most rainforest

trees on birds and mammals that disperse seeds as a critical phase of tropical tree life

cycles (Howe 1986). The point is to shape foraging routes of fruit-eating animals by

providing plantings that offer cover and/or food, and consequently facilitate seed dispersal into fenced habitat islands that serve as stepping stones among forest remnants for "countryside" plants and animals capable of existing in agricultural landscapes (Daily et al. 2001). We use well-established recruits of tree species dispersed into experimental exclosures to determine whether fruit-eating birds and bats have comparable roles in promoting forest succession over the first years of ecological restoration.

Our study considers processes of effective dispersal, which involves removal of seeds from parent trees to sites where germination, establishment and survival are possible (Schupp et al. 2010). Our test of dispersal agency is done in fenced plots that are either left unplanted to simulate natural succession, planted with 12 species of native wind-dispersed trees, or planted with 12 species of native animal-dispersed trees as assisted succession. Patterns of seed fall offer insight into potential composition of regenerating forests (Martínez-Garza et al. 2009), but the vast majority of seeds fail to establish as recruits (Harms et al. 2000). Relevant to this study, succession in abandoned tropical pastures is slow even if seeds of forest trees arrive (Holl 1998, de la Peña-Domene et al. 2013). Established recruits are useful predictors of colonization dynamics in early-successional habitats where scattered seedlings are not clumped in dense cohorts near fruiting adults of the same species. In restoration plots far from seed sources, high density-dependent mortality from insects, pathogens, vertebrates and cohort competition is less likely to take a toll on seedlings than in clusters of seeds or seedlings near adults of the same species in forest. Sparsely-distributed seeds and young plants are more likely to succumb to haphazard seed predation by ants and rodents, xeric field conditions, and competition from aggressive grasses.

We test the null hypothesis that fruit-eating birds and bats play comparable roles in promoting tree and shrub recruitment over the first 76 months of experimental restoration in an agricultural-rainforest mosaic in southern Veracruz, Mexico. Some fruit-eating birds and bats forage locally within pastures; others commute long distances to and from feeding areas (Guevara and Laborde 1993). Differences in dispersal roles might be expected because fruit-eating bats in agricultural Neotropical landscapes are thought to depend heavily on small-seeded trees, many of which are pioneer trees and shrubs of early succession (Muscarella and Fleming 2007). In contrast, toucans and other medium-sized to large birds feed on many fruits of trees of late-secondary and primary forest, and carry seeds hundreds of meters to and from feeding sites in forest remnants, isolated trees, and isolated stands of trees (Guevara and Laborde 1993, Graham 2001). Of particular interest is accumulation of established recruits of pioneer and later-successional tree species that we did not plant in replicated plots that simulate assisted as compared with natural succession.

4.2 METHODS

The study site was in an agricultural mosaic in the Los Tuxtlas Region of southeastern Veracruz, ~ 1 km NE of the nearest edge of the Los Tuxtlas Biological Station (González Soriano et al. 1997). Topography is complex, with thin, eroded sandy loam of heterogeneous depth (median 18.5 cm, range 5 - > 70 cm) over rocky volcanic deposits (Tobon et al. 2011, Martínez-Garza et al. 2013b). Nearby rainforests, including at least 372 plant species of dbh $\geq$ 2.5 cm, are described elsewhere (Bongers et al. 1988, Arroyo-Rodríguez et al. 2009a). The landscape is highly fragmented; excluding epiphytes, 81% of plant species occur in fragments of $\leq$ 5 ha, and ~ 70% occur in $\leq$ 5 such fragments (Arroyo-Rodríguez et al. 2009a). Mean annual temperature and rainfall are 27º C and ~ 4900 mm,

respectively. Normal dry seasons from March to May sometimes extend as droughts

through June (e.g. Martínez-Garza et al. 2013b). The landscape hosts ~ 72 species of

resident fruit-eating birds and 24 species of fruit-eating bats, most of which frequent

forest, forest fragments, and mosaic habitats (Estrada et al. 1993, Guevara and Laborde

1993).

The12 ha site where we conducted the study was cattle pasture embedded in an

agricultural mosaic of rainforest, isolated trees, and living fences. In August 2006 we

established 24 fenced 30 x 30 m plots separated by 35 m of active cattle pasture arranged in

a 3 x 8 grid (central GPS point 18° 35′ 43.64″ N, 95° 06′ 06.29″ W). Eight exclosures were

planted with 12 seedlings of 12 native animal-dispersed species (> 10 cm high), and eight

with 12 native wind-dispersed species with 12 seedlings each (de la Peña-Domene et al.

2013, Martínez-Garza et al. 2013a). Eight unplanted controls represented minimal

manipulation (fencing) to simulate natural succession on abandoned land. Matrices

between exclosures remained closely cropped grasses. Here we compared fenced

unplanted controls with fenced plantings of native trees.

Criteria for designations of tree successional status and dispersal category are consistent

with general practice (Howe 1986, Estrada et al. 1993). Rationales for departures are

outlined in supplemental materials (Appendix 4.8.1), along with botanical authorities and

plant families (Appendix table 4.8.2). Species recruited since 2006 as seedlings, saplings or

rapidly-growing trees are listed with references of published reports indicating primary

dispersal agents and pioneer or later-successional status (Appendix table 4.8.2). An outlier

plot of wind-dispersed trees is not included here (deeper, wetter soil with tree growth far

ahead of 23 other plots). Recruits $\geq$ 10 cm high were recorded every 4-6 months from month 16 (October 2007) through month 76 (January 2013) after cattle exclusion.

This experiment is expected to span 30 years. Prior publications address legacy effects through month 24 after cattle exclusion (Howe et al. 2010), and recruitment rates as functions of successional status (early or late) and general dispersal mode (animal or wind) through month 60 (de la Peña-Domene et al. 2013). Both studies pre-date detectable differences in effects of bats and birds. Other reports address patterns of seed fall (Martínez-Garza et al. 2009), soil characteristics (Tobon et al. 2011), mortality of planted seedlings (Martínez-Garza et al. 2013b) and growth of planted trees over the first 30-42 months (Martínez-Garza et al. 2013a).

Primary analytical tools are mixed-model repeated-measures randomized-block ANOVAs. Pioneer and later-successional species and recruitment densities are evaluated independently. Independent variables include time (month of census or initial and final census), dispersal agent (birds, bats or both) and treatment (planted or unplanted), with interactions. F-statistics are considered significant when the Bonferroni adjustment is significant at $P \leq$ 0.05. Statistics are accomplished with SAS and Systat 13.

4.3 RESULTS

4.3.1 Recruitment over time

Distinctively different patterns of recruitment by dispersal category and life history emerged over time (Figure 4.6.1, Tables 4.7.1 and Appendix table 4.8.2). Densities of pioneer species increased from 0.0007 species m^{-2} to 0.0023 m^{-2} from 16 to 76 months after cattle exclusion ($P <$ 0.0001). Significant differences existed in overall contribution of dispersal categories to pioneer-species densities ($P <$ 0.0001), but interaction of dispersal

category of pioneer species densities with time was not significant (Figure 4.6.1*A*, *P* = 0.80).

Individual densities of pioneer recruits increased from a mean of 0.0014 m^{-2} in 2007 to

0.005 m^{-2} in 2013 (*P* < 0.0001). Significant overall differences by dispersal category of

individual pioneer recruits existed (*P* < 0.0001), but again the interaction of dispersal

category with time was not significant (Figure 4.6.1*C*, *P* = 0.11).

Patterns of recruitment of later-successional species differed dramatically by dispersal

category. Species densities of later-successionals increased four-fold from the initial to the

final census (from 0.0005 m^{-2} in 2007 to 0.0023 m^{-2} in 2013, *P* < 0.0001). At 76 months after

cattle exclusion, species densities of later-successional trees and shrubs dispersed

primarily by birds were five times higher than those dispersed by both bats and birds,

with a significant interaction of dispersal category with time (Figure 4.6.1*B*, *P* < 0.0001).

Later-successional species dispersed by bats alone were not present. Recruitment of

species dispersed by birds appeared to inflect upward 60 months after cattle exclusion,

and showed a strong and statistically significant inflection upward at 70 months as many

planted animal-dispersed trees matured and bore fruit. The number of individual later-

successional recruits increased ~ seven-fold over the same period (0.0018 recruits m^{-2} to

0.012 m^{-2}, *P* < 0.0001), with a significant interaction of dispersal category with time (Figure

4.6.1*D*, *P* < 0.0001). Significant upward inflection of individual recruits dispersed by birds

was evident at 48 months after cattle exclusion and increased dramatically with time as

planted trees matured.

4.3.2 Initial and final recruit densities

The net contribution to recruitment of surviving individuals of pioneer and later-successional species dispersed primarily by birds was substantial, whereas the net effect of recruited species dispersed by both birds and bats or primarily by bats alone was not (Figure 4.6.2, Appendix table 4.8.2). Individual recruit densities of pioneer tree and shrub species dispersed by both birds and bats or bats alone differed little between 16 and 76 months after cattle exclusion, while pioneers dispersed by birds increased in both planted and control plots (Figure 4.6.2*A*). Recruits of later-successional species dispersed by birds alone increased in both planted and control treatments, with the most dramatic increases in planted plots (Figure 4.6.2*B*).

4.4 DISCUSSION

Tropical forests generate and maintain most of the biodiversity of terrestrial ecosystems on Earth (Dirzo and Raven 2003), yet are rapidly succumbing to habitat loss as forested land is converted to pasture and crops (Fahrig 2003, Fearnside 2005). Less appreciated is re-forestation of land that is at least temporarily useless for agriculture (Chazdon 2003). For land under human domination, reasonable priorities for conservation and restoration of tropical biodiversity include restoring dispersal processes that: (a) conserve biological diversity in highly altered agricultural landscapes by maintaining habitat heterogeneity, and (b) accelerate recovery of biodiversity and ecosystem services when land is abandoned to secondary succession.

Planned heterogeneity in agricultural landscapes contributes to both connectivity and recovery after abandonment. When land is too valuable to be released from agriculture, tree islands maintain substantial biological diversity and connectivity between large forest

remnants, fragments, and restorations undergoing succession (Harvey and Haber 1998, Benayas et al. 2008, Arroyo-Rodríguez et al. 2009b, Cole et al. 2010). Ultimately, mixed stands of reproductive trees serve as regeneration nuclei for forest recovery if depleted agricultural land is abandoned (Benayas et al. 2008, Holl et al. 2011). Here we report roles of birds and bats that mediate colonization of experimental controls and plantings by tree species other than those we planted.

Later-successional trees rarely establish from seed in early successional habitats unless agents of dispersal are attracted to sites that coincidently have shade, moisture and protection from livestock (Martínez-Garza and Howe 2003). Fenced and planted plots offer conditions that increase chances of germination and growth (Butler et al. 2008, de la Peña-Domene et al. 2013). It is also likely that scattered incoming recruits establish under a broader range of conditions than they would in closed forests. In early successional habitats, shade-tolerant species arrive by chance and establish and grow where it is physically possible, without much influence of competition from conspecifics until self-thinning occurs at sapling or young-adult stages. Until then many recruited species experience the advantage of few nearby conspecific competitors (Comita et al. 2010). In a managed setting intended to optimize diversity of pollen and seed movement among plots and fragments over 20-30 years, trees will grow large enough to reproduce, but are unlikely to reach a size sufficient to prevent several other species from reaching maturity in a given plot.

In our experiment, influx of species from the landscape was notable. Ninety-four percent of animal-dispersed recruits that survived to 76 months were of species other than those that we planted, including 17 later-successional and 12 of 14 pioneer species. Most pioneer

recruits in experimental plots were of shrubs and trees that produced fruits eaten by a wide variety of birds, bats, and terrestrial mammals. Pioneer recruits of *Cecropia obtusifolia, Conostegia xalapensis,* and *Witheringia nelsonii* evidently established from seeds brought by opportunistic bird or bat foragers on fruits of naturally regenerating *C. xalapensis* and planted *C. obtusifolia* and *Ficus yoponensis*. The latter two are heavily used by both birds and bats (Guevara and Laborde 1993, Medellin and Gaona 1999b, Galindo-Gonzalez et al. 2000, Slocum 2001). More species of fruit-eating birds than fruit-eating bats occur in the Los Tuxtlas landscape, but it is still remarkable that seedling recruits of later-successional shrubs and trees were of species dispersed primarily by birds, and to a lesser extent by both birds and bats. None were dispersed by bats alone. Densities of some pioneer recruits dispersed primarily by birds increased slightly over time in both planted and control plots; densities of later-successional trees dispersed primarily by birds increased significantly in controls and dramatically in planted plots.

Use of fruiting trees by bats and birds is to a degree context-specific. *Ficus yoponensis*, a planted free-standing fig in our experiment with fruits available on at least three small adult trees within 48 months after cattle exclusion, is a "bat fruit" in diverse Central American forests (Kalko et al. 1996). The species is heavily used by both birds and bats in disturbed settings: as many as 45 species of fruit-eating birds forage in isolated *F. yoponensis* at Los Tuxtlas (Guevara and Laborde 1993). From 48-76 months after cattle exclusion, 5-36 individual planted *Cecropia obtusifolia* produce fruit at any given time. Some congeners of this species are more bat- than bird-dispersed (e.g. *C. peltata* versus *C. obtusifolia* in reference (Medellin and Gaona 1999a), $\chi^2 = 56.0$, df = 1, $P < 0.001$). In pastures

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at Los Tuxtlas, *C. obtusifolia* is both bird- and bat-dispersed (Galindo-Gonzalez et al. 2000), while in forest a menagerie of arboreal mammals also eat the fruits (Estrada et al. 1984).

In the present experiment, legacy effects faded over time. A few older recruits, including reproductive *C. obtusifolia* and *Trema micrantha* and sapling *Bursura simaruba*, appeared in the plots directly after fencing, reflecting legacies of seeds brought to figs or other fruiting trees that were cut during site preparation (Howe et al. 2010). Additional recruits appeared several months to years after fencing, well beyond dormancy periods for most Neotropical tree seeds (Norden et al. 2009, Dalling et al. 2011). With either immediate or delayed germination, seedling survival poorly reflected seed arrival; germination, establishment, and recruitment to seedling and later life-history stages were context-dependent (Howe 1986, Schupp et al. 1989, Howe et al. 2010, Schupp et al. 2010, Reid and Holl 2013). For seeds that did arrive, xeric conditions and thick grass suppressed establishment of tree seedlings, killed seedlings that did establish, and likely intensified density-dependent mortality of seeds and young seedlings under perches.

Planted stands reduce both seed and establishment limitation. Birds that potentially disperse seeds are more likely to forage in clumps of shrubs or trees than in open areas, stay longer in larger than smaller stands of woody vegetation, and regurgitate or defecate more seeds in tree islands than in the open (Benayas et al. 2008, Butler et al. 2008, Laborde et al. 2008, Cole et al. 2010). Moreover, seedlings fare better in shade where grass is at least partially suppressed than in the open (Slocum 2001, de la Peña-Domene et al. 2013). As expected, greater seed arrival and enhanced seedling survival substantially accelerate succession in planted stands as compared with unassisted natural succession in controls. Over the first six to seven years of restoration in the Los Tuxtlas landscape, fruit-eating

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birds are far more effective mediators of succession by later-successional trees and shrubs from forest than fruit-eating bats.

Only a small proportion of seeds resulted in established seedlings in pasture plots. Early in the present experiment, we reported seed input of woody plants into fenced plots > 90 m from forest of one seed in 10 m^{-2} month^{-1} (Martínez-Garza et al. 2009), a rate that increased substantially as succession occurred (de la Peña-Domene, unpublished data). After 76 months of cattle exclusion, actual recruit density in controls averaged ~ one shrub or tree recruit 100 m^{-2}, indicating immense mortality of seeds or young seedlings. In contrast, planted plots averaged ~ one recruit 16 m^{-2}. These densities were well below those under large fenced figs in a pasture landscape (Laborde et al. 2008), and were below what would be expected in a mature closed-canopy continuous forest (Metz 2012). After more than six years of succession in cattle exclosures, recruited seedlings were still sparse.

With the exception of common pioneers, species planted in our experiment are in higher densities than occur in nature. High densities differentially affect survival of planted species, and will likely bias early recruitment in favor of species *other* than those that we planted (Janzen 1970, Clark et al. 2013). In the 50 ha Barro Colorado Island forest-dynamics plot, for instance, interactions among trees range from little thinning of older juveniles and adults to strong negative density-dependence among conspecifics, but with much less sensitivity to proximity of heterospecifics (Comita et al. 2010). In our experiment, we expect substantial thinning of saplings and young adults of most planted species. High densities of most planted species are also likely to directly or indirectly impede recruitment of conspecific seedlings.

Scattered colonists from forests will likely have a different dynamic. Plots with 120 m of edge admit diffuse light, explaining high establishment of pioneers during the first five years of cattle exclusion (de la Peña-Domene et al. 2013). A question is whether deepening shade will repress recruitment of pioneers and allow later-successional species to establish in small (900 m^2) stands. At least to established seedling, sapling and in some case adult stages, this is occurring, with a clear increase in establishment of later-successional species between 60 and 76 months, and little recruitment of most planted or early-recruited pioneers that are fruiting in planted plots.

It is too early to know whether the imbalance of bird- versus bat-dispersed later-successional recruits will persist. In addition to dispersal of small-seeded pioneers, bats disperse many large-seeded, late-successional species in continuous forest in both the Old- and New-World Tropics (Giannini and Kalko 2004). Large neotropical fruit bats (e.g. *Artibeus lituratus,* up to 70 g) carry *Dipteryx* (Fabaceae) fruits weighing > 20 g for hundreds of meters, but even small fruit bats (e.g. *Artibeus watsoni*, 12 g) disperse a variety of tree seeds > 20 mm long in extensive forest (Melo et al. 2009). Fruit-eating bats large enough to carry fruits of substantial size (1-20 g) are common in the Los Tuxtlas landscape (Estrada et al. 1993). Bats may play a greater role in recruitment of later-successional trees as planted figs mature and continue to grow in size and fecundity. The absence of a substantial role of dispersal of later-successional trees by bats during the first six years of experimental restoration is surprising.

Our study has significant implications for maintaining biodiversity in human-dominated landscapes. Mixed-species plantings potentially maintain and locally increase "countryside diversity" of tropical plants and animals that are capable of persisting in or

moving through human-dominated landscapes (Daily et al. 2001, Hughes et al. 2002).

Managed landscape heterogeneity is not a panacea for preservation of all tropical

diversity; some fruit-eating animals fail to reach or thrive in forest islands, with adverse

consequences for those tree species that depend on them (e.g. Cordeiro and Howe 2003).

Extensive remnants preserve tropical flora and fauna that require old-growth habitats, and

preserve sources of plant and animal colonists of land that is eventually released from

crops and pasture (Gibson et al. 2011). For the half of the rainforest biome that has been

deforested during the last century, however, the goal of preserving all rainforest

biodiversity is unrealistic. Many rare species with limited geographical distributions are

almost certainly already extinct (Hubbell et al. 2008). But others of conservation interest

are potentially spared by heterogeneous habitats. For instance, in our experiment 38 well-

established (25-52 cm tall) seedlings of endemic IUCN red-listed vulnerable *Ocotea*

uxpanapana (Lauraceae) are present, as are 20 well-established (14-800 cm tall)

Tetrorchidium rotundatum (Euphorbiaceae; de la Peña-Domene, unpublished data), a

widespread animal-dispersed tree that is nonetheless endangered in Mexico. A realistic

goal for maintenance and recovery of substantial tropical biodiversity is to sustain and re-

establish dispersal processes that preserve or create as much habitat heterogeneity and

connectivity as rural economies permit.

Habitat islands left as remnants or planted as stepping stones in matrices between forest

remnants serve a variety of functions. Connectivity preserves landscape species richness at

large scales (Turner and T. Corlett 1996, Damschen et al. 2006, Kramer et al. 2008);

stepping-stone forest islands retain and restore some tree species, serve as foraging and

breeding refuges of mobile animals, contribute reproductive connectivity among trees

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through pollen exchange and seed dispersal, and provide nuclei of forest regeneration if land is released from agriculture. To date, increased understanding of the importance of seed dispersal by animals has had little effect on conservation or restoration in the tropics (McConkey et al. 2012). Creating heterogeneity with corridors and stepping-stone tree islands cannot preserve all tropical diversity; a key objective should be to retain as many uniquely important tree species and dispersal agents as possible. With half of the tropical rainforest biome cleared at least once in the last 100 years, forest conservation and restoration using birds and mammals that transport seeds should become a central theme in ecology of this century.

4.5 LITERATURE CITED

Arroyo-Rodríguez, V., J. C. Dunn, J. Benítez-Malvido, and S. Mandujano. 2009a. Angiosperms, Los Tuxtlas Biosphere Reserve, Veracruz, Mexico. Check List, Campinas 5:787-799.

Arroyo-Rodríguez, V., E. Pineda, F. Escobar, and J. Benitez-Malvido. 2009b. Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. Conservation Biology 23:729-739.

Benayas, J. M. R., J. M. Bullock, and A. C. Newton. 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and the Environment 6:329-336.

Bongers, F., J. Popma, J. M. Delcastillo, and J. Carabias. 1988. Structure and Floristic Composition of the Lowland Rain-Forest of Los-Tuxtlas, Mexico. Vegetatio 74:55-80.

Butler, R., F. Montagnini, and P. Arroyo. 2008. Woody understory plant diversity in pure and mixed native tree plantations at La Selva Biological Station, Costa Rica. Forest Ecology and Management 255:2251-2263.

Clark, C. J., J. R. Poulsen, and D. J. Levey. 2013. Roles of Seed and Establishment Limitation in Determining Patterns of Afrotropical Tree Recruitment. Plos One 8:e63330.

Cole, R. J., K. D. Holl, and R. A. Zahawi. 2010. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecological Applications 20:1255-1269.

Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric Density Dependence Shapes Species Abundances in a Tropical Tree Community. Science 329:330-332.

Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. Proceedings of the National Academy of Sciences of the United States of America 100:14052-14056.

Corlett, R. T. 2011. Impacts of warming on tropical lowland rainforests. Trends in ecology & evolution (Personal edition) 26:606-613.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6:51-71.

Chazdon, R. L. 2008. Beyond deforestation: Restoring forests and ecosystem services on degraded lands. Science 320:1458-1460.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica. Ecological Applications 11:1-13.

Dalling, J. W., A. S. Davis, B. J. Schutte, and A. Elizabeth Arnold. 2011. Seed survival in soil: interacting effects of predation, dormancy and the soil microbial community. Journal of Ecology 99:89-95.

Damschen, E. I., N. M. Haddad, J. L. Orrock, J. J. Tewksbury, and D. J. Levey. 2006. Corridors Increase Plant Species Richness at Large Scales. Science 313:1284-1286.

de la Peña-Domene, M., C. Martínez-Garza, and H. F. Howe. 2013. Early recruitment dynamics in tropical restoration. Ecological Applications 23:1124-1134.

Dirzo, R., and P. H. Raven. 2003. Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137-167.

Estrada, A., R. Coates-Estrada, D. M. Jr, S. Montiel, and D. Curiel. 1993. Patterns of Frugivore Species Richness and Abundance in Forest Islands and in Agricultural Habitats at Los Tuxtlas, Mexico. Vegetatio 107/108:245-257.

Estrada, A., R. Coates-Estrada, and C. Vazquez-Yanes. 1984. Observations on Fruiting and Dispersers of Cecropia obtusifolia at Los Tuxtlas, Mexico. Biotropica 16:315-318.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: History, Rates, and Consequences

Deforestación en la Amazonía Brasileña: Historia, Tasas y Consecuencias. Conservation Biology 19:680-688.

Galindo-Gonzalez, J., S. Guevara, and V. J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14:1693-1703.

Giannini, N. P., and E. K. V. Kalko. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. Oikos 105:209-220.

Gibson, L., T. M. Lee, L. P. Koh, B. W. Brook, T. A. Gardner, J. Barlow, C. A. Peres, C. J. A. Bradshaw, W. F. Laurance, T. E. Lovejoy, and N. S. Sodhi. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478:378-381.

González Soriano, E., R. Dirzo, and R. C. Vogt. 1997. Historia natural de los Tuxtlas. 1. edition. Universidad Nacional Autónoma de México Instituto de Ecología, México.

Graham, C. H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology 15:1789-1798.

Guevara, S., and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio 107/108:319-338.

Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature 404:493-495.

Harvey, C. A., and W. A. Haber. 1998. Remnant trees and the conservation of biodiversity in Costa Rican pastures. Agroforestry Systems 44:37-68.

Holl, K. D. 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? Restoration Ecology 6:253-261.

Holl, K. D., R. A. Zahawi, R. J. Cole, R. Ostertag, and S. Cordell. 2011. Planting Seedlings in Tree Islands Versus Plantations as a Large-Scale Tropical Forest Restoration Strategy. Restoration Ecology 19:470-479.

Howe, H. F. 1986. Seed dispersal by fruit-eating birds and mammals. Page 189 *in* D. R. Murray, editor. Seed dispersal. Academic Press New York.

Howe, H. F., Y. Urincho-Pantaleon, M. de la Peña-Domene, and C. Martinez-Garza. 2010. Early seed fall and seedling emergence: precursors to tropical restoration. Oecologia 164:731-740.

Hubbell, S. P., F. He, R. Condit, L. Borda-de-Água, J. Kellner, and H. ter Steege. 2008. How many tree species are there in the Amazon and how many of them will go extinct? Proceedings of the National Academy of Sciences 105:11498-11504.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 2002. Conservation of tropical forest birds in countryside habitats. Ecology Letters 5:121-129.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501-527.

Kalko, E. K. V., E. A. Herre, and C. O. Handley. 1996. Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. Journal of Biogeography 23:565-576.

Kramer, A. T., J. L. Ison, M. V. Ashley, and H. H. F. 2008. The Paradox of Forest Fragmentation Genetics. Conservation Biology 22:878 - 885.

Laborde, J., S. Guevara, and G. Sanchez-Rios. 2008. Tree and shrub seed dispersal in pastures: The importance of rainforest trees outside forest fragments. EcoScience 15:6-16.

Lamb, D., P. D. Erskine, and J. A. Parrotta. 2005. Restoration of degraded tropical forest landscapes. Science 310:1628-1632.

Martínez-Garza, C., F. Bongers, and L. Poorter. 2013a. Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? Forest Ecology and Management 303:35-45.

Martínez-Garza, C., A. Flores-Palacios, M. De La Peña-Domene, and H. F. Howe. 2009. Seed rain in a tropical agricultural landscape. Journal of Tropical Ecology 25:541-550.

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Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. Journal of Applied Ecology 40:423-429.

Martínez-Garza, C., W. Tobon, J. Campo, and H. F. Howe. 2013b. Drought mortality of tree seedlings in an eroded tropical pasture. Land Degradation & Development:287-295.

McConkey, K. R., S. Prasad, R. T. Corlett, A. Campos-Arceiz, J. F. Brodie, H. Rogers, and L. Santamaria. 2012. Seed dispersal in changing landscapes. Biological Conservation 146:1-13.

Medellin, R. A., and O. Gaona. 1999a. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica 31:478-485.

Medellin, R. A., and O. Gaona. 1999b. Seed Dispersal by Bats and Birds in Forest and Disturbed Habitats of Chiapas, Mexico1. Biotropica 31:478-485.

Melo, F. P. L., B. Rodriguez-Herrera, R. L. Chazdon, R. A. Medellin, and G. G. Ceballos. 2009. Small Tent-Roosting Bats Promote Dispersal of Large-Seeded Plants in a Neotropical Forest. Biotropica 41:737-743.

Metz, M. R. 2012. Does habitat specialization by seedlings contribute to the high diversity of a lowland rain forest? Journal of Ecology 100:969-979.

Muller-Landau, H. C., and B. D. Hardesty. 2005. Seed dispersal of woody plants in tropical forests: concepts, examples and future directions. Pages 267-309 *in* D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley, editors. Biotic interactions in the tropics: their role in the maintenance of species diversity Ecological Reviews

Muscarella, R., and T. H. Fleming. 2007. The Role of Frugivorous Bats in Tropical Forest Succession. Biological Reviews 82:573-590.

Norden, N., M. I. Daws, C. Antoine, M. A. Gonzalez, N. C. Garwood, and J. Chave. 2009. The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. Functional Ecology 23:203-210.

Reid, J. L., and K. D. Holl. 2013. Arrival ≠ Survival. Restoration Ecology 21:153-155.

Schupp, E. W., H. F. Howe, C. K. Augspurger, and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology 70:562-564.

Schupp, E. W., P. Jordano, and J. M. Gomez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333-353.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology 82:2547-2559.

Tobon, W., C. Martinez-Garza, and J. Campo. 2011. Soil responses to restoration of a tropical pasture in Veracruz, south-eastern Mexico. Journal of Tropical Forest Science 23:338-344.

Turner, I. M., and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology & Evolution 11:330-333.

Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. Trends in Ecology & Evolution 17:379-386.

Wunderle, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management 99:223-235.

4.6 FIGURES
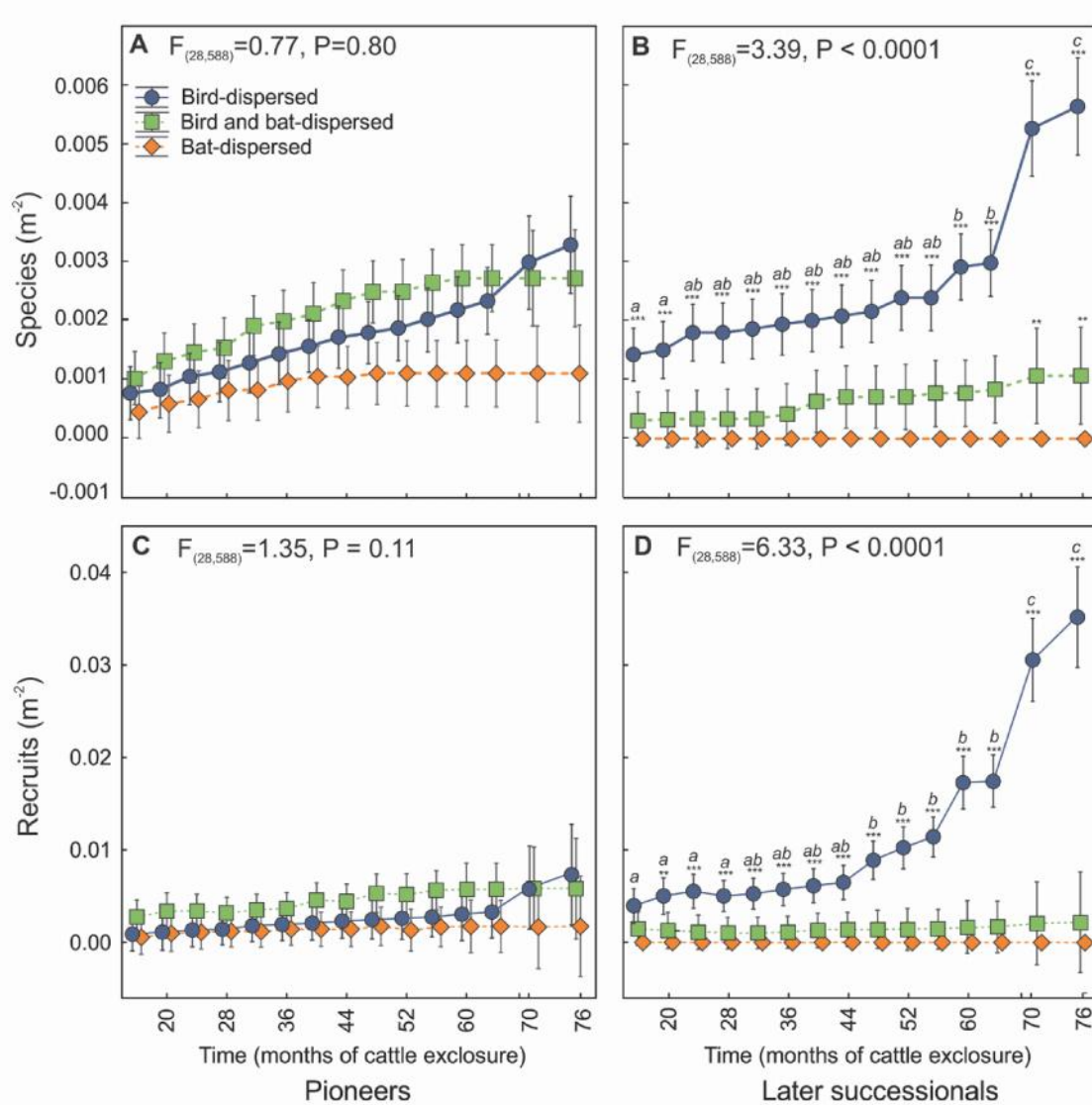
Figure 4.6.1 Changes in density of recruited species and individuals by dispersal group over time. Shown are (a) pioneer species, (b) later-successional species, (c) pioneer individuals, (d) later-successional individuals. Blue circles indicate primarily bird-dispersed, green squares both bird- and bat-dispersed, and rust diamonds primarily bat-dispersed species. Asterisks indicate differences between dispersal categories in the same time period. Anova statistics indicate disperser category by time interactions. Letters show differences for bird-dispersed later-successional trees from one time period to the next using conservative bonferroni post-hoc tests ($p < 0.05$). Shown are means and 95% confidence intervals.
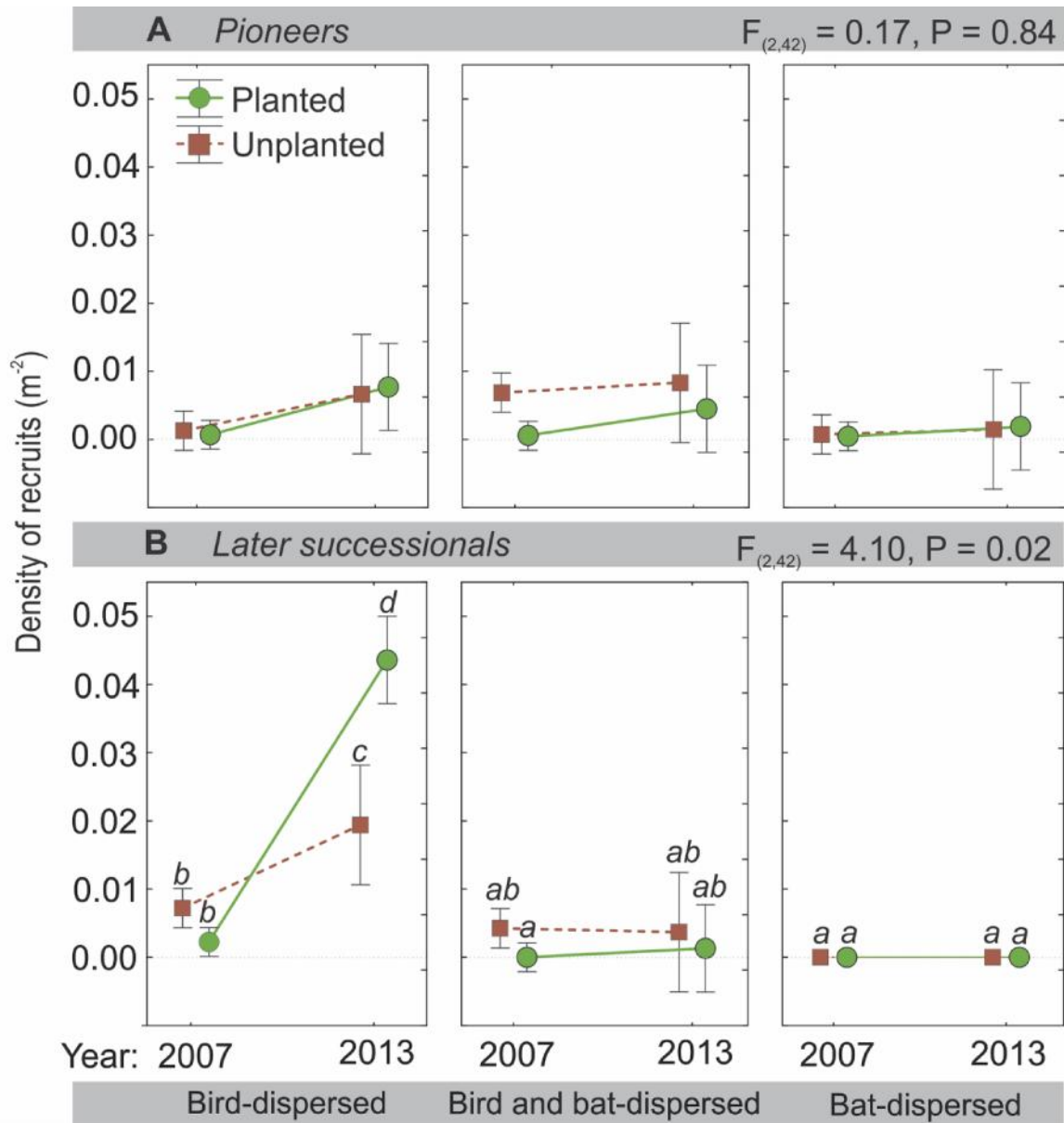
Figure 4.6.2 Net change in densities of recruited individuals by successional status and dispersal mode. Dispersal mode is indicated for (a) densities of pioneers and (b) densities of later-successional recruits. Blue circles indicate plantings, green squares unplanted controls. Anova statistics indicate disperser category by time interaction. Letters indicate differences between recruits in 2007 as compared with 2013 (bonferroni adjustments, p < 0.05). Shown are means and 95% confidence intervals.

Table 4.7.1. Mixed-model ANOVA of species and recruit densities over time. Fixed effects are dispersal mode (bird, bat or both) and planting treatment (planted or unplanted control), with time (16 to 76 months) after cattle exclusion.

			Pioneer		*Later successional*	
Species density	num.d.f.	den.d.f.	F-value	P	F-value	P
Time	14	294	6.97	***	6.64	***
Dispersal	2	42	92.77	***	834.85	***
Planting	1	21	10.42	**	25.62	***
Time*Dispersal	28	588	0.77		3.39	***
Time*Planting	14	294	0.48		0.36	
Dispersal*Planting	2	42	14.91	***	26.04	***
Disp*Time*Planting	28	588	0.26		0.46	
Recruit density	num.d.f.	den.d.f.	F-value	P	F-value	P
Time	14	294	8.05	***	9.31	***
Dispersal	2	42	118.25	***	820.48	***
Planting	1	21	28.57	***	21.71	***
Time*Dispersal	28	588	1.35		6.33	***
Time*Planting	14	294	1.19		1.04	
Dispersal*Planting	2	42	38.16	***	44.09	***
Disp*Time*Planting	28	588	0.14		0.89	

$P < 0.005$ **, $P < 0.0001$ ***

4.8 APPENDICES

Appendix 4.8.1 **Criteria for designating dispersal modes and successional status.**

Dispersal modes of species that recruit to our experimental plots are generally consistent

with recognized suites of fruit characters: scentless "bird fruits" are colorful red, blue,

yellow, black, or multicolored, while musty or otherwise odorous "bat fruits" are white,

yellowish, or green (Van der Pijl 1982). These syndromes are also generally consistent with

designations by botanists working in the Los Tuxtlas region (Guevara 1994, Ibarra-

Manriquez et al. 2001). Because dispersal syndromes do not always predict actual use by

fruit-eating animals in a given landscape, examples of direct observations are given to at

least the genus level when observed usage confirms or contradicts expectations from

syndromes. Records of direct use of species reflect different levels of accuracy. Most

useful are unusual simultaneous comparisons of dispersal of plant taxa by birds and bats

in southern Mexico (Medellin and Gaona 1999, Galindo-Gonzalez et al. 2000). For instance,

colorful fruits of strangler figs (subgenus Urostigma of Ficus) fit the bird-dispersed

syndrome, while green fruits of free-standing figs (subgenus Pharmacoscya of Ficus)

suggest the bat or arboreal mammal syndrome. Empirical collections from seed traps that

distinguish diurnal from nocturnal seed deposition in southern Mexico indicate broad

overlap of use of both fig subgenera by birds and bats (Medellin and Gaona 1999, Galindo-

Gonzalez et al. 2000). Moreover, many tree taxa recruited in our plots would additionally

be dispersed by primates or by other arboreal or terrestrial mammals in continuous forest,

but these potential dispersal agents are absent from plots (primates) or are unlikely to be

frequent visitors that cross open pastures for the first years of this experiment before

planted trees produce substantial quantities of fruit. We expect regular use by terrestrial

omnivores that eat fruit and defecate intact seeds (Canis latrans, Didelphis spp., Nasua

narica, Procyon lotor) when planted and eventually recruited animal-dispersed trees produce large enough fruit crops to draw the animals across open ground. Here, aside from the general treatise on dispersal syndromes (Van der Pijl 1982) or supplements to botanical references (Guevara 1994, Ibarra-Manriquez et al. 2001), we minimize compounding "syndrome errors" by citing representative studies that report data from direct observation of foraging animals, fecal samples, or from seed traps that distinguish day and night catches. Records that report animal use of the same species that we report are in bold type, those to the same genus in regular type. Many papers that cite use of a species indicate use of congeneric plants as well. Where quantitative comparisons are available with day and night measures of bird and bat use of tree and shrub species (Medellin and Gaona 1999, Galindo-Gonzalez et al. 2000), trees are considered "bird-" or "bat-" dispersed if the number of seeds in one category is > 4X seeds in the other category. In other cases we take the weight of evidence. For instance Clidemia is generally listed as bird-dispersed (Table S1). Occasional use of C. octona by bats is known (Appendix 8 of (Fleming 1988). Designations of successional stage are open to interpretation. Early pioneer species colonize open areas and live up to 30 years ("tempranos") or as late-pioneers up to 60 years ("tardios") of Martinez-Ramos (1985). Most of these are listed as "pioneers" by Ibarra-Manriquez et al. (2001), the term that we adopt. We use "later-successional" to conform to designations of "persistent" by Ibarra-Manriquez et al. (2001) and "nomadas" and "tolerantes" of Martinez-Ramos (1985). Published designations of successional stage of Piper amalago and Stemmadenia donnell-smithii are contradictory; we regard them as pioneers because both are rapidly-maturing early colonists of open ground in our landscape. Both also occur in mature forest. In addition to the animal-dispersed species listed (Table S1), seedlings of 13 wind-dispersed trees and shrubs also

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recruited in plots. These included five planted species (Albizia purpusii Britton & Rose,

Cedrela ordorata L., Heliocarpus appendiculatus Turcz, Ochroma pyramidale (Cav. ex

Lam.) Urb., Vochysia guatemalensis Donn. Sm.), of which all but C. odorata seeded

between 60 and 76 months after cattle exclosure. Other wind-dispersed recruits included

five pioneers (Eupatorium galeottii B.L. Rob., Cnidoscolus multilobus Pax. I. M. Johnston,

Heliocarpus donnell-smithii Rose, Lippia microphylla Cham., Trichospermum galeottii

(Turcz.) Kosterm) and two later-successional trees (Cordia alliodora (Ruiz & Pav.) Oken,

Dalbergia glomerata Hemsl.). Cordia alliodora conspecifics were close to isolated pasture

conspecifics and stumps of conspecifics cut during site preparation.

References

Fleming, T. H. 1988. The short-tailed fruit bat. University of Chicago Press, Chicago.

Galindo-Gonzalez, J., S. Guevara, and V. J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14:1693-1703.

Guevara, S., J. Meave., P. Moreno-Casasola, J. Laborde y S. Castillo. 1994. Vegetación y flora de potreros en la sierra de Los Tuxtlas, México. Acta Botanica Mexicana 28:1-27.

Ibarra-Manriquez, G., M. M. Ramos, and K. Oyama. 2001. Seedling functional types in a lowland rain forest in Mexico. American Journal of Botany 88:1801-1812.

Martínez-Ramos, M. 1985. Claros, ciclos vitales de los árboles tropicales y la regeneración natural de las selvas altas perennifolias. Pages 191-239 in A. G.-P. S. d. Amo, editor. Investigaciones sobre la Regeneración de las Selvas Altas en Veracruz, México Editorial Alhambra Mexicana, S.A., México, D.F.

Medellin, R. A., and O. Gaona. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica 31:478-485.

Van der Pijl, L. 1982. Principles of dispersal in higher plants. Springer-Verlag, Berlin.

Appendix 4.8.2

Table 4.8.2. Dispersal mode and successional status of recruited species, including references for published reports.

Designations of dispersal agents are generally consistent with recognized dispersal syndromes [1-3], indicated in italics. Field confirmations with direct observations of plants identified to the genus level are numbered in regular font; field confirmations identified to species are in bold. Ambiguous identifications of plants are checked with the Mexican National Herbarium at Universidad Nacional Autónoma de México.

Species (family)	Primary dispersal	Life form	References
Later Successional			
Alchornea latifolia Sw. (Euphorbiaceae)	Birds	Tree	*1,2,3,7,8,9,10,11,12,13*
Bursera simaruba (L.) Sarg. (Burseraceae)	Birds	Tree	*1,2,3,4,7,11,14*
Clusia flava Jacq. (Clusiaceae)	Birds	Tree	*1,3,7,8,11,13,15,16*
[a] *Coccoloba hondurensis* Lundell (Polygonaceae)	Both	Tree	*2,3,6,11,16,17,18*
Cupania glabra Sw. (Sapindaceae)	Birds	Tree	*1,2,3,4,5,7,9,11,13,16*
Cymbopetalum bailonii R. E. Fr. (Annonaceae)	Birds	Tree	*1,2,3,4,14,19*
[b] *Ficus aurea* Nutt. (Urostigma, Moraceae)	Both	Tree	*2,3,5,7,9,10,11,12,13,15, 16,17,18,20,21,22,see 4*
[c] *Nectandra ambigens* (S.F. Blake) C.K. Allen (Lauraceae)	Birds	Tree	*2,3,9,10,11,16*
Ocotea uxpanapana T. Wendt & van der Werff (Lauraceae)	Birds	Tree	*2,3,7,11,13,16*
[d] *Pleuranthodendron lindenii* (Turcz.) Sleumer (Salicaceae)	Birds	Tree	*1,2,3,11,12,16*
[e] *Pseudolmedia oxyphyllaria* Donn. Sm. (Moraceae)	Both	Tree	*2,3,22,23*
Psychotria limonensis K. Krause (Rubiaceae)	Birds	Shrub	*1,2,3,9,11,12,13,15, 16,24,25,26*
[f] *Rollinia jimenezii* Saff. (Annonaceae)	Both	Tree	*1,2,3,11,18*
[g] *Sapindus saponaria* L. (Sapindaceae)	Both	Tree	*2,6,11,17*
[h] *Sapium nitidum* (Monach.) Lundell (Euphorbiaceae)	Birds	Tree	*1,2,3,11,16,28,29*
Tabernaemontana alba Mill. (Apocynaceae)	Birds	Tree	*1,2,3,11,16*
Tetrorchidium rotundatum Standl.(Euphorbiaceae)	Both	Tree	*2,3,4,15*
Trichilia martiana C. DC. (Meliaceae)	Birds	Tree	*1,2,3,11,16,30,31,32*
Trophis mexicana (Liebm.) Bureau (Moraceae)	Birds	Tree	*1,2,3,11,14,16,23*
Pioneer			
Acacia cornigera (L.) Wild. (Fabaceae)	Birds	Both	*2,3,33*
Cecropia obtusifolia Bertol. (Cecropiaceae)	Both	Tree	*2,3,4,5,6,7,8,9,10,12,13,16,*

			17,18,21,22,34,35-38
Cestrum racemosum R. & P.(Solanceae)	Birds	Tree	*1,2,3,9,10,11,16, cf.18,38*
Clidemia spp. (Melastomataceae)	Birds	Shrub	*1,6,10,11,15,25,26*
Conostegia xalapensis (Kunth H.B.K.) G. Don ex DC. (Melastomataceae)	Both	Both	*2,3,4,10,11,15,16, 26,34,36,39*
Hampea nutricia Fryxell (Malvaceae)	Birds	Tree	*1,2,3,10,11,16,36*
Miconia spp. (Melastomaceae)	Birds	Both	*1,7,8,9,10-13,15, 16,24-26,32,36,40*
Piper amalago L. (Piperaceae)	Bats	Tree	*1,2,3,4,5,6,11,16,17,21, 22,35,36,37,38,41,42*
Piper hispidum Sw. (Piperaceae)	Bats	Both	*1,2,3,4,5,6,11,16,17,21, 22,35,36,37,38*
[i] *Piper umbellatum* L. (Piperaceae)	Bats	Shrub	*2,4,5,6,11,16,17,21,22, 26,35,36,37,38*
[j] *Psidium guajava* L. (Myrtaceae)	Both	Tree	*1,3,6,11,17,35,44-47*
Stemmadenia donnell-smithii (Rose) Woodson (Apocynaceae)	Birds	Tree	*1,2,3,11,16,48,49,50*
[k] *Trema micrantha* (L.) Blume (Ulmaceae)	Birds	Tree	*1,2,8,11,13,16, 51, cf. 4,22*
Witheringia nelsonii (Fern.) Hunz. (Solanaceae)	Both	Shrub	*5,10,11,15,16,36, 38,52,53*

[a] An unusual compilation of difficult-to-find literature on bat frugivory is Lobova et al. (18).

[b] syn. *Ficus tecolutensis* (Liebm.) Miq.

[c] Sometimes eaten by large bats (*Artibeus jamaicensis*, 22).

[d] Included here is closely-related (*Hasseltia*,11,14,16) with broad avian disperser assemblages.

[e] Mostly primates in forest (e.g. 22), which are not present in pasture plots.

[f] syn. *Rollinia mucosa* (Jacquin) Baillon.

[g] Direct observations are scarce. Note 27.

[h] syn. for *Sapium sebiferum* (L.) Roxb. is *Triadica sibifera* (L.) Small.

[i] Included with syn. *Pothomorphe umbellata* (L.) Miqu. in a tight *Piper auritum* clade (43). *Piper auritum* fruits are eaten by birds (16,26,36), but where direct quantitative comparisons are available seeds are overwhelmingly dispersed by bats (4,5).

[j] This is an extreme generalist, with records including birds, bats, other mammals, and reptiles (48).

[k] Bats sometimes eat this fruit (4,22), but it appears to be mostly bird-dispersed.

References

1. Van der Pijl L (1982) Principles of dispersal in higher plants. 3rd edition. Berlin: Springer-Verlag.

2. Ibarra-Manriquez G, Martinez-Ramos M, Oyama K (2001). Seedling functional types in a lowland rain forest in Mexico. American Journal of Botany 88(10):1801-1812.

3. Guevara S, Meave J, Casasola PM, Laborde J, Castillo S (1994) Vegetacion y flora de potreos en la Sierra de los Tuxtlas, Mexico. Acta Botanica Mexicana 28: 1-27.

4. Galindo-Gonzalez J, Guevara S, Sosa VJ (2000) Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology 14: 1693–1703.

5. Medellin R A, Gaona O (1999) Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica 31(3): 478-485.

6. Fleming TH (1988) The short-tailed fruit bat. Chicago: University of Chicago Press.

7. Carlo TA, Collazo JA, Groom MJ (2003) Avian fruit preferences across a Puerto Rican forested landscape: Pattern consistency and implications for seed removal. Oecologia 134: 119-131.

8. Skutch AF (1980) Arils as food of tropical American birds. Condor 82(1): 31– 42.

9. Kessler-Rios MM, Kattan GH (2012) Fruits of Melastomataceae: phenology in Andean forest and role as a food resource for birds. Journal of Tropical Ecology 28: 11-21.

10. Blake JG, Loiselle BA (1992) Fruits in the diets of neotropical migrant birds in Costa Rica. Biotropica 24(2a):200-210.

11. Snow DW (1981) Tropical frugivorous birds and their food plants: A world survey.Biotropica 13(1):1–4.

12. Greenberg R (1981) Frugivory in some migrant tropical forest wood warblers. Biotropica 13(3): 215-223.

13. Galetti M, Laps R, Pizo MA (2000) Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic forest of Brazil. Biotropica 32(4b): 842-850.

14. Foster MS (2007) The potential of fruit trees to enhance converted habitats for migrating birds in southern Mexico. Bird Conservation International 17: 45-61.

15. Boyle WA, Conway CJ, Bronstein JL (2011) Why do some, but not all, tropical birds migrate? A comparative study of diet breadth and fruit preference. Evolutionary Ecology 25: 219–236.

16. Wheelwright NT, Haber WA, Murray KG, Guindon G (1984) Tropical fruit-eating birds and their food plants – a survey of a Costa Rican lower montane forest. Biotropica 16: 173-192.

17. Greenhall AM (1957) Food preferences of Trinidad fruit bats. Journal of Mammalogy 38(3): 409-410.

18. Lobova TA, Geiselman CK, Mori SA (2009) Seed Dispersal by Bats in the Neotropics (New York Botanical Society, New York).

19. Coates-Estrada R, Estrada A (1988) Frugivory and seed dispersal in *Cymbopetalum baillonii* (Annonaceae) at Los Tuxtlas, Mexico. Journal of Tropical Ecology 4: 157-162.

20. Guevara S, Laborde J (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Vegetatio107/108: 319-338.

21. Bonaccorso FJ (1979) Foraging and reproductive ecology in a Panamanian bat community. Bulletin of the Florida State Museum, Biological Sciences 24: 359-408.

22. Estrada A, Coates-Estrada R, Vasquez-Yanes C, Orozco-Segovia A (1984) Comparison of frugivory by howling monkeys (*Alouatta palliata*) and bats (*Artibeus jamaicensis*) in the tropical rain forest of Los Tuxtlas, Mexico. American Journal of Primatology 7: 3-13.

23. Lancaster DA (1964) Life history of the Boucard tinamou in British Honduras Part I: Distribution and general behavior. Condor 66(3): 165– 181.

24. Poulin B, Wright SJ, LeFebvre G, Calderon O (1999) Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. Journal of Tropical Ecology 15: 213-227.

25. Morales-Betancourt JA, Castano-Villa CJ, Fonturbel FE (2012) Resource abundance and frugivory in two manakin species (Aves: Pipridae) inhabiting a reforested area in Colombia. Journal of Tropical Ecology 28: 511-514.

26. Loiselle BA (1990) Seeds in droppings of tropical fruit-eating birds: importance of considering seed composition. Oecologia 82: 494-500.

27. Carlquist S (1966) The biota of long-distance dispersal. III. Loss of dispersibility in the Hawaiian flora. Brittonia 18(4): 310-335.

28. Renne IJ, Barrow W C., Jr., Randall LA., Bridges, WB, Jr (2002) generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. Diversity and Distributions 8: 285–295.

29. Aslan CE (2011) Implications of newly-formed seed-dispersal mutualisms between birds and introduced plants in northern California, USA. Biological Invasions 13: 2829–2845.

30. Leck CF (1969) Observations of birds exploiting a Central American fruit tree. Wilson Bulletin 81: 264-269.

31. Foster MS, McDiarmid RW (1983) Nutritional value of the aril of *Trichilia cuneata*, a bird-dispersed fruit. Biotropica 15(1): 26-31.

32. Poulin B, LeFebvre G, McNeil R (1992) Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology 73(6): 2295-2309.

33. Janzen DH (1966) Coevolution of ants and acacias in Central America. Evolution 20(3): 249-275.

34. Cole RJ, Holl KD, Zahawi RA (2010) Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecol Appl 20(5): 1255-1269.

35. Garcıa-Estrada C, Damon A, Sanchez-Hernandez C, Soto-Pinto L, Ibarra-Nunez, G (2012) Diets of frugivorous bats in montane rain forest and coffee plantations in southeastern Chiapas, Mexico. Biotropica 44(3): 394 – 401.

36. Palmeirim JM, Gorchov DL, Stoleson S (1989) Trophic structure of a neotropical frugivore community: Is there competition between birds and bats? Oecologia 79:403-411

37. Dinerstein E (1986) Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. Biotropica 18(4): 307-318.

38. Goncalves da Silva AG, Gaona O, Medillin RA (2008) Diet and trophic structure in a community of fruit-eating bats in Lacandon Forest, Mexico. Journal of Mammalogy 89(1): 43–49.

39. Castro-Luna AA, Vinicio J, Sosa VJ (2009) Consumption of *Conostegia xalapensis* fruits and seed dispersal of *Coussapoa oligocephala* by the nectarivorous bat *Hylonycteris underwoodi* Thomas, 1903 (Chiroptera: Phyllostomidae). Studies on Neotropical Fauna and Environment 44: 137-139.

40. Loiselle BA, Blake JG (1999) Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. Ecology 80(1): 330-336.

41. Fleming TH, Heithaus ER, Sawyer WB (1977) An experimental analysis of the food location behavior of frugivorous bats. Ecology 58(3): 619-627.

42. Fleming TH (1981) Fecundity, fruiting pattern, and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub. Oecologia 51: 42-46.

43. Jaramillo MA, Manos PS (2001) Phylogeny and patterns of floral diversity in the genus Piper (Piperaceae). American Journal of Botany 88(4): 706–716.

44. Jordaan LA, Johnson SD, Downs CT (2011) The role of avian frugivores in germination of seeds of fleshy-fruited invasive alien plants. Biological Invasions 13: 1917–1930.

45. Jordaan, LA, Johnson SD, Downs CT (2012) Wahlberg's epauletted fruit bat (*Epomophorus wahlbergi*) as a potential dispersal agent for fleshy-fruited invasive alien plants: effects of handling behaviour on seed germination. Biological Invasions 14: 959–968.

46. Berens DG, Farwig N, Schaab G, Bohning-Gaese KB (2008) Exotic guavas are foci of forest regeneration in Kenyan farmland. Biotropica 40(1): 104-112.

47. Heleno RH, Olesen MN, Vargas P, Traveset A (2013) Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. Proceedings of the Royal Society B 280: 20122112. http://dx.DOI.org/10.1098/rspb.2012.2112.

48. McDiarmid RW, Ricklefs RE, Foster MS (1977) Dispersal of *Stemmadenia donnell-smithii* (Apocynaceae) by birds. Biotropica 9: 9–25.

49. Coates-Estrada R, Estrada A,.Merritt D Jr (1993) Foraging by parrots (*Amazona autumnalis*) on fruits of *Stemmadenia donnell-smithii* (Apocynaceae) in the tropical rain forest of Los Tuxtlas, Mexico. Journal of Tropical Ecology 9: 121-124.

50. Shweiki S, Howe HF (2009) Regeneration of deep-forest *Stemmadenia donnell-smithii* (Apocynaceae) at Los Tuxtlas, Mexico. Plant Species Biology 24: 225-228.

51. Vazquez-Yanes C (1998) *Trema micrantha* (L.) Blume (Ulmaceae): A promising neotropical tree for site amelioration of deforested land. Agroforestry Systems 40: 97-104.

52. Murray KG (1988) Avian seed dispersal of three neotropical gap-dependent plants. Ecological Monographs 58(4): 271-298.

53. Murray KG, Russell S, Picone CM, Winnett-Murray K, Sherwood W, Kuhlmann ML (1994) Fruit laxatives and seed passage rates in frugivores: Consequences for plant reproductive success. Ecology 75(4): 989-
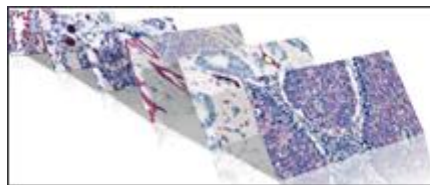
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CHAPTER V

5. RESTORATION OF FUNCTIONAL CONNECTIVITY SUPPORTS
OCOTEA UXPANAPANA, **AN ENDEMIC VULNERABLE TREE**

Restoration of functional connectivity supports *Ocotea uxpanapana*, an endemic vulnerable tree

Marinés de la Peña-Domene, Emily Minor and Henry F. Howe

5.1 INTRODUCTION

Throughout the tropics, vast expanses of rainforest are being converted into cattle grazing pasture, leaving small forest fragments scattered among farms and pastures (Houghton 1994, Ojima et al. 1994, Montagnini and Jordan 2005). Isolated populations often lose genetic variability (Honnay et al. 2005), reducing their ability to adapt to environmental changes and increasing risk of local extinction (Frankham and Ralls 1998, Davis and Shaw 2001, Opdam and Wascher 2004, Frankham 2005). Therefore, subsistence of many plant and animal populations depends on their ability to re-colonize distant habitat patches (Gustafson and Gardner 1996). Many authors have suggested that increasing landscape connectivity through corridors or stepping stones (Metzger 1997, Pascual-Hortal and Saura 2007, Uezu et al. 2008, García-Feced et al. 2011, among others, Saura et al. 2014) is one of the best options for conservation in the face of habitat loss and climate change (reviewed in Heller and Zavaleta 2009). Strategic networks of connected patches allow for dispersal between environmentally similar habitats (Alagador et al. 2012) and may counterbalance the effects of fragmentation by broadening species distributions, rescuing genetically isolated populations, and assisting in conservation of animal and plant species. Landscape connectivity may also increase the success of restoration efforts (Tambosi et al. 2014), although little empirical work has tested this idea yet.

The vast majority of Neotropical rain forest plants are dispersed by animals (e.g. Frankie et al. 1974, Howe 1977, Howe and Smallwood 1982, among others). However, when animal movement is impeded by fragmentation, then animal-mediated seed dispersal is also obstructed and animal-dispersed plants do not reach neighboring vegetation patches. In this situation, seeds and seedlings fail to escape disproportionate mortality near parent trees and face negative density-dependent effects that forfeit species success (i.e. Janzen-Connell effect, Janzen 1970, Connell 1971). Large-seeded trees are especially vulnerable to fragmentation because they tend to be dispersed by larger animals (Wheelwright 1985, Cramer et al. 2007, Markl et al. 2012). Larger animals are often low in number due to hunting and they rarely cross open pastures from one patch to the other (Terborgh et al. 2008, Melo et al. 2010, Markl et al. 2012). This is the case of *Ocotea uxpanapana* T. Wendt & van der Werff, a globally vulnerable tree (WCMC 1998) that is endemic to Los Tuxtlas and the Uxpanapa in the south of Veracruz, Mexico. This species has a large seed (~1.5 cm wide, Wendt and Werff 1987) and is locally dispersed by large birds like toucans (*Ramphastos sulfuratus*) and oropendolas (*Psarocolius montezuma*).

The Los Tuxtlas region of southern Mexico is arguably the northern-most tropical rain forest on the American continent. Remaining rainforest constitutes a small area of high biodiversity in a landscape severely fragmented by grazing and other agricultural activities (87% of the original vegetation is deforested, Dirzo and Garcia 1992). A clear restoration goal here, like in many tropical forests, is to facilitate or restore dispersal processes that recover and maintain the biodiversity that can coexist with people. (Turner and T. Corlett 1996, Daily et al. 2001, Hughes et al. 2002, Vandermeer and Perfecto 2007).

Gaining connectivity between forest patches within the agricultural matrix is a key component to conservation of animal and plant species.

We established experimental plots with the objective of testing if dispersal processes can be manipulated to accelerate natural succession. Previous work in these plots showed that planted plots had many more recruited species than unplanted control plots (de la Peña-Domene et al. 2013). In particular, we found a dramatic increase in later-successional bird-dispersed species, many of which are known to be large-seeded, primary forest trees (de la Peña-Domene et al. 2014). Here we take a spatially-explicit approach to examine the potential of high diversity restoration plots in active pastures to act as stepping-stones that functionally reconnect populations of *O. uxpanapana* in the agricultural landscape. We hypothesized that planted plots will play a dual role in shaping the recruitment patterns of the focal species, by first attracting large birds to fruiting trees and second by providing suitable conditions for germination and survival of *Ocotea*. We ask (1) what is the importance of local canopy cover and seed dispersal probability on establishment of *Ocotea* seedlings, and (2) whether restoration efforts alter seed dispersal pathways.

5.2 MATERIALS AND METHODS

5.2.1 Study site

The Los Tuxtlas Biological Station (LTBS) lies within a reserve of 640 ha of lowland tropical rain forest, continuous with 3,500 additional ha, in the state of Veracruz, southeast Mexico (description and botanical check-list in González -Soriano *et al*. 1997). The forest has a closed canopy ~ 35 m high. Mean annual temperature and rainfall are 27° C and 4,900 mm, respectively. Normal dry season extends from March to May, and rainy season

from June to February. Soil is sandy loam classified as vitric andosols originating from basalt and andesite mixed with volcanic ash and clay (González-Soriano *et al*. 1997). Our site is a cow pasture that has been intensively grazed for 30-40 years, embedded in a mosaic of primary and secondary forest.

5.2.2 Experimental design

In July - August 2006, we established twenty-four fenced plots (30 x 30 m) separated by 35 m of pasture (central GPS point 18º 35' 43.64'' N, 95º 06' 06.29'' W) adjacent to the LTBS and oriented NE to the Gulf of Mexico (Figure 5.7.1). The 3 x 8 grid was fenced-in pasture of an agricultural Colony. Plots are 500 to 1200 m from the edge of the LTBS, with the SW corner 90 m from privately-owned secondary forest. Individually tagged seedlings of 24 tropical tree species from 15 families were planted in plots from September 2006 to February 2007, and re-planted from August to November 2007 as needed (more details in de la Peña-Domene et al. 2013, Martínez-Garza et al. 2013). Eight plots were planted with seedlings of animal-dispersed species, eight with seedlings of wind-dispersed species, and eight left as fenced, unplanted controls.

Starting in June 2007, we recorded naturally-recruited seedlings in the plots every 4 months for the first five years and every 6 months from 2012 to 2014. The total area assessed in each plot was 563 m² for planted plots and 676 m² for control plots, excluding space used for bat net lanes, seed traps, 0.5 m² spaces for planted seedlings (in planted plots), and a 1 m buffer inside the fences that cows could reach. The total sampled area was 14,415 m². Seedlings 10 cm high were the smallest size that could reliably be found. Seedlings < 10 cm high, when found and tagged rarely survived to the next census and are not considered in the analysis here. The present study reports on naturally recruited

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seedlings of *O. uxpanapana*, which were first found in 2011 and have increased to 38 well-established saplings in the plots. We also recorded the location of all reproductive *O. uxpanapana* adults in the surrounding 100 hectares.

5.2.3 Canopy cover and seed dispersal probability

We measured canopy cover in each plot and across the broader landscape. At the plot level, we took 12 high-contrast canopy photos per plot, counted the luminous pixels in each photo and subtracted them from the total number of pixels over all photos, and calculated the mean percent cover openness per plot. Photos were taken in July 2012. For the remaining landscape (outside of the plots), we digitized individual trees and the surrounding forest from a 2009 aerial photograph and converted this to a binary raster data layer with 1m resolution in ArcMap 10.1.

We estimated seed dispersal probability into each plot in several different ways. We calculated Euclidean distance and accumulated-costs of the least cost path (LCP) distance from all reproductive adults to each plot. We used the Cost Path tool in ArcMap 10.1 to identify the LCP. The path is based on a resistance or "cost" surface, which describes the cost a disperser might incur as it traveled across the landscape. Because *Ocotea* is primarily dispersed by large forest birds, we assumed that increased canopy cover would be associated with lower dispersal costs (or higher rewards, in terms of potential food resources). Therefore, our cost surface assigned a value of (100 – (% canopy cover) to each 1m² pixel, resulting in a travel cost of zero in pixels with complete canopy cover and a cost of 100 in pixels with no canopy cover. The cost path tool attempts to find the path from point A (each reproductive adult, in our case) to point B (each study plot) that accumulates the minimum total cost. These paths may wind across the landscape in non-linear ways

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and are particularly influenced by the presence of tree canopy (Figure 1). Once we calculated Euclidean distance and the LCP from all reproductive adults, we identified the minimum Euclidean distance and the minimum LCP for each plot. These minimum values represent distance to the nearest reproductive adult and were used in our models as estimates of seed dispersal probability. As a third estimate of seed dispersal probability, we counted the number of times a LCP passed through each plot on route to other plots. LCPs, and the number of times a path crossed through each plot, were calculated before restoration (assigning a canopy cover value of 0 to all plots) and after restoration, so we could examine how restoration might alter dispersal paths across the landscape.

5.2.4 Statistical analysis

We first used correlation analysis to examine the relationships between abundance of seedlings in each plot and the canopy cover and dispersal probability variables. The relationships with canopy cover, minimum Euclidean distance, and minimum least cost distance were non-linear, so we transformed those variables by taking their natural log before including them. We then used multiple linear regression to evaluate the combined importance of local canopy cover openness, seed dispersal probability, and their interaction term on *Ocotea* establishment. We selected the dispersal probability variable that was most strongly correlated with number of *Ocotea* seedlings to include in the model. Canopy cover and dispersal probability were natural-log transformed and then centered (by subtracting the mean from each observation) before calculating the interaction term to reduce collinearity and increase interpretability of their regression slopes. Finally, to answer questions about the effect of restoration on seed dispersal routes, we performed a repeated measures ANOVA with number of crossing routes as a dependent variable and

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experimental treatment (control, plantings of wind-dispersed species, and plantings of animal-dispersed species) and time (before or after restoration) as independent variables. We used Statistica 7 and R for all statistical analysis.

5.3 RESULTS

The number of *Ocotea* seedlings increased as a function of canopy cover and decreased as a function of Euclidean distance, LCP distance, and number of crossing routes through each plot (Table 5.6.1). All predictor variables were significantly correlated with number of *Ocotea* seedlings (Table 5.6.1), although the LCP distance was the most strongly correlated dispersal probability variable. Therefore, LCP distance was included with canopy cover in the multiple linear regression model. The regression coefficients for canopy cover, LCP distance, and their interaction term were all significant (Table 5.6.1); together, these three variables explained 73% (adjusted r^2 = 0.69) of the variability in number of *Ocotea* seedlings. Figure 5.7.2 reveals an apparent threshold at 35% canopy openness, above which *Ocotea* seedlings rarely established. *Ocotea* seedling abundance was highest in plots with both low canopy openness (i.e., planted plots) and short LCP distances. Seedlings were occasionally found in plots with high openness but short LCP distances, or in plots with long LCP distances but low canopy openness.

Prior to restoration, there were no differences between treatments in the number of indirect routes crossing plots (mean 3 ± SD 5 routes per plot). After 7 years of establishment and growth, both planting types significantly increased in the number of indirect routes crossing through the plantings from the potential parent trees to the destination plot ($F_{(2, 21)}$ = 8.04, P < 0.005, figure 5.7.3) compared to unplanted control plots. Plots planted with wind-dispersed trees increased from 2.5 ± 3.1 to 18 ± 15 routes per plot,

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while plots planted with animal-dispersed trees increased from 2.1 ± 2.9 to 14.4 ± 6.3 routes per plot. Unplanted control plots decreased from 4.5 ± 5.5 to1.1 ± 2 routes per plot. Additionally, in the pre-restoration scenario, there was no correlation between the number of established seedlings and the number of crossing routes. As a function of an increase in the use of plots as stepping stones, measured by the number of dispersal routes crossing per plot, the number of *Ocotea* seedlings also increased (r = 0.54, P < 0.005).

5.4 DISCUSSION

We have shown that small plots of planted trees can serve two important functions in restoration of tropical forest. First, the canopy cover in these plots creates a suitable environment for establishment of later-successional tree species. Second, by altering dispersal pathways and reducing movement cost for seed dispersers, canopy cover increases influx of large, animal-dispersed seeds into plots and restores functional connectivity to the landscape. This is important first because many large-seeded trees are particularly affected by the isolation of forest fragments and the decrease of forest fruit-eating animals. When dispersers of large seeds are absent, seeds are prevented from successfully recruiting seedlings either near fruiting trees or in more distant sites undergoing succession (Markl et al. 2012). As a result, the evolutionary trajectories and community composition of tropical forest may change as disperser guilds change (Galetti et al. 2013).

A major threat to *Ocotea uxpanapana* is habitat loss and fragmentation (World Conservation Monitoring Centre, 1998). Fragmentation reduces the movement of animals that disperse its seeds. Forest disturbances that alter the community of animal seed-dispersers indirectly affect the plant community. A consequence is that habitat fragmentation, logging and

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hunting decrease the number of seeds that leave a forest and colonize new sites (Markl et al. 2012). Larger animals are often the first to be extirpated. The result is that disturbed forests lose those agents that disseminate large seeds and often large quantities of small seeds. Decline in abundance and distribution of larger animals can eventually lead to the decline of large-seeded trees like *Ocotea*.

Small vegetation patches have the potential to act as stepping-stones across the landscape and increase movement through fragmented habitat. The spatial arrangement and quality of those habitat patches can significantly affect the rate of movement through them (Collingham and Huntley 2000). In our case, we found toucans and oropendolas foraging even in small plots (unpublished data); they proved to be efficient dispersers for *Ocotea* and other large-seeded species. Another study in the area reported toucans ranging widely over isolated trees, fragments, living fences and riparian strips (Graham 2001). However, a third study from Los Tuxtlas did not find toucans in small plots of 2 to 3 ha, but only in plots larger than 22 ha, independent of their proximity to forest patches (Melo et al. 2010). We suggest that these different findings are likely due to patch quality, rather than patch size. Our patches contained high-diversity plantings that offered food resources and shelter and likely were very attractive to the large frugivores. Therefore, an approach that restores habitat and functional connectivity for seed-dispersers may be more likely to succeed in the long-term.

Assessing established seedlings, we learn about effective dispersal, which means that the seeds are dispersed into a patch with adequate conditions for germination and establishment (Schupp 1993, Schupp et al. 2010, de la Peña-Domene et al. 2014). In this study, evaluating established seedlings allowed us to infer dispersal routes of large birds

that disperse *Ocotea* seeds. Our approach very likely underestimated the spatial extent of seed movement (Kamm et al. 2010), but nonetheless revealed patterns of actual recruit from dispersed seeds. Increasing dispersal probabilities was one of the factors that explained the recruitment pattern of *Ocotea* seedlings. However, as shown in figure 5.7.2, an evident threshold at 65% canopy cover was revealed, which also accounted for the variation in the recruitment patterns of the species.

One important aspect in restoring functional connectivity is addressing the spatial arrangement of the restored patches in relation to existing forest remnants (Tambosi et al. 2014). Another relevant aspect is the quality of the restored vegetation patches (DeClerck et al. 2010). Yet more importantly, it is the functions and interactions that are regained through the restored vegetation that make them an efficient conservation strategy (Ceccon and Varassin 2014).

Establishment of *O. uxpanapana* seedlings is related to higher dispersal probabilities measured as least-cost path. Although Euclidian distances were also correlated with seedling establishment, this metric ignored the ecological cost of movement for an individual. On the other hand, using the accumulative costs given by the LCP offered more information on the difficulty associated with traversing different parts of a landscape for potential dispersers. Higher costs represented species-specific factors that impede movement such as greater mortality risk, energetic cost or a behavior of fear (Etherington and Penelope Holland 2013). Euclidian distances from potential parent trees to restoration plots remained the same, while the costs of the paths evidently decreased as a function of restoration treatments.

Creating scattered mosaic of habitat fragments that facilitate species dispersal has been proposed as a way to counterbalance negative effects of fragmentation (Martínez-Garza and Howe 2003, Baum et al. 2004, Kramer et al. 2008, Uezu et al. 2008). Spatial arrangement of suitable patches in the landscape can significantly affect the migration rates of animals and hence, animal-dispersed plants (Collingham and Huntley 2000). Our study reveals a substantial change in dispersal routes as an effect of maturing mixed-species planted plots. Plantings serve as stepping-stones and decrease the cost paths from parent trees to the scattered plots. Dispersal processes are inherent to landscape features that can affect species in different ways. The functionality of such networks strongly depends on their effect on the mobility of species (Ricketts 2001, Bélisle and St. Clair 2002, Schtickzelle and Baguette 2003, Bélisle 2005). For some organisms, creating small vegetation patches that work as stepping-stones arranged though the landscape can increase mobility in fragmented landscapes (Collingham and Huntley 2000). Organisms that are able to move through the matrix will benefit from structurally disconnected vegetation patches.

Our results may apply other large-seeded tree species facing similar constraints. Other later-successional bird-dispersed species like *Nectandra ambigens*, *Virola guatemalensis* and *Pseudolmedia oxyphyllaria* also colonize our experimental plantings (de la Peña-Domene et al. 2014). All are large-seeded species of primary forest. The capacity of species to exploit the opportunities created by networks of stepping-stone patches largely species-specific. Species with other life histories, as pioneers are likely to show opposite patterns. Dispersal probabilities of pioneers dispersed by animals might increase as a function of restoration, yet the increasingly dense canopy cover may prevent them from successfully establishing

in shade. This suggests that species assemblages traversing fragmented landscapes experience a spatial filtering process that drives long-term changes in community composition.

Together, croplands and pastures are dominant terrestrial biomes, occupying close to 40% of land surface (Ramankutty and Foley 1999, Asner et al. 2004, Foley et al. 2005). Persistence of global biodiversity relies upon the ability of species to move large distances across human-modified landscapes (Schloss et al. 2012). Stepping-stone patches may be crucial in this effort. Our study demonstrates the importance of stepping-stone patches for a globally vulnerable species, *Ocotea uxpanapana*. Small mixed-species forest plots attracts seed dispersers and alters their movements through a cow pasture, restoring functional connectivity and accelerating restoration efforts. Recognizing the actual role of networks of stepping-stone patches in providing connectivity is of paramount importance to develop effective conservation strategies that help mitigate the impacts of global change on biodiversity.

5.5 LITERATURE CITED

Alagador, D., M. Trivino, J. O. Cerdeira, R. Bras, M. Cabeza, and M. B. Araujo. 2012. Linking like with like: optimising connectivity between environmentally-similar habitats. Landscape Ecology 27:291-301.

Asner, G. P., A. J. Elmore, L. P. Olander, R. E. Martin, and A. T. Harris. 2004. Grazing systems, ecosystem responses and global change. Annual Review of Environment and Resources 29:261-299.

Baum, K. A., K. J. Haynes, F. P. Dillemuth, and J. T. Cronin. 2004. The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85:2671-2676.

Bélisle, M. 2005. Measuring landscape connectivity: The challenge of behavioral landscape ecology. Ecology 86:1988-1995.

Bélisle, M., and C. C. St. Clair. 2002. Cumulative effects of barriers on the movements of forest birds. Conservation Ecology 5.

Ceccon, E., and I. G. Varassin. 2014. Plant-pollinator interactions in ecosystems restoration.*in* M. Benítez, O. Miramontes, and A. Valiente-Banuet, editors. Frontiers in Ecology, Evolution and Complexity. CopIt-arXives, Mexico City.

Collingham, Y. C., and B. Huntley. 2000. Impacts of habitat fragmentation and patch size upon migration rates. Ecological Applications 10:131-144.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands.

Cramer, J. M., R. C. G. Mesquita, and G. Bruce Williamson. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation 137:415-423.

Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica. Ecological Applications 11:1-13.

Davis, M. B., and R. G. Shaw. 2001. Range Shifts and Adaptive Responses to Quaternary Climate Change. Science 292:673-679.

de la Peña-Domene, M., C. Martínez-Garza, and H. F. Howe. 2013. Early recruitment dynamics in tropical restoration. Ecological Applications 23:1124-1134.

de la Peña-Domene, M., C. Martínez-Garza, S. Palmas-Pérez, E. Rivas-Alonso, and H. F. Howe. 2014. Roles of Birds and Bats in Early Tropical-Forest Restoration. Plos One 9:e104656.

DeClerck, F. A. J., R. Chazdon, K. D. Holl, J. C. Milder, B. Finegan, A. Martinez-Salinas, P. Imbach, L. Canet, and Z. Ramos. 2010. Biodiversity conservation in human-

modified landscapes of Mesoamerica: Past, present and future. Biological Conservation 143:2301-2313.

Dirzo, R., and M. C. Garcia. 1992. Rates of Deforestation in Los Tuxtlas, a Neotropical Area in Southeast Mexico. Conservation Biology 6:84-90.

Etherington, T., and E. Penelope Holland. 2013. Least-cost path length versus accumulated-cost as connectivity measures. Landscape Ecology 28:1223-1229.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global consequences of land use. Science 309.

Frankham, R. 2005. Genetics and extinction. Biological Conservation 126:131-140.

Frankham, R., and K. Ralls. 1998. Conservation biology: Inbreeding leads to extinction. Nature 392:441-442.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881-919.

Galetti, M., R. Guevara, M. C. Côrtes, R. Fadini, S. Von Matter, A. B. Leite, F. Labecca, T. Ribeiro, C. S. Carvalho, R. G. Collevatti, M. M. Pires, P. R. Guimarães, P. H. Brancalion, M. C. Ribeiro, and P. Jordano. 2013. Functional Extinction of Birds Drives Rapid Evolutionary Changes in Seed Size. Science 340:1086-1090.

García-Feced, C., S. Saura, and R. Elena-Rosselló. 2011. Improving landscape connectivity in forest districts: A two-stage process for prioritizing agricultural patches for reforestation. Forest Ecology and Management 261:154-161.

Graham, C. H. 2001. Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. Conservation Biology 15:1789-1798.

Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77:94-107.

Heller, N. E., and E. S. Zavaleta. 2009. Biodiversity management in the face of climate change: A review of 22 years of recommendations. Biological Conservation 142:14-32.

Honnay, O., H. Jacquemyn, B. Bossuyt, and M. Hermy. 2005. Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytologist 166:723-736.

Houghton, R. A. 1994. The worldwide extent of land-use change. Bioscience 44:305-313.

Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539-550.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201-228.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 2002. Conservation of tropical forest birds in countryside habitats. Ecology Letters 5:121-129.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501-527.

Kamm, U., F. Gugerli, P. Rotach, P. Edwards, and R. Holderegger. 2010. Open areas in a landscape enhance pollen-mediated gene flow of a tree species: evidence from northern Switzerland. Landscape Ecology 25:903-911.

Kramer, A. T., J. L. Ison, M. V. Ashley, and H. H. F. 2008. The Paradox of Forest Fragmentation Genetics. Conservation Biology 22:878 - 885.

Markl, J. S., M. Schleuning, P. M. Forget, P. Jordano, J. E. Lambert, A. Traveset, S. J. Wright, and K. Böhning-Gaese. 2012. Meta-Analysis of the Effects of Human Disturbance on Seed Dispersal by Animals. Conservation Biology 26:1072-1081.

Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on species loss. Journal of Applied Ecology 40:423-429.

Martínez-Garza, C., W. Tobon, J. Campo, and H. F. Howe. 2013. Drought mortality of tree seedlings in an eroded tropical pasture. Land Degradation & Development:287-295.

Melo, F. P. L., E. Martínez-Salas, J. Benítez-Malvido, and G. Ceballos. 2010. Forest fragmentation reduces recruitment of large-seeded tree species in a semi-deciduous tropical forest of southern Mexico. Journal of Tropical Ecology 26:35-43.

Metzger, J. P. 1997. Relationships between landscape structure and tree species diversity in tropical forests of South-East Brazil. Landscape and Urban Planning 37:29-35.

Montagnini, F., and C. F. Jordan. 2005. Tropical Forest Ecology: The Basis For Conservation And Management. Springer Berlin Heidelberg New York, Netherlands.

Ojima, D. S., K. A. Galvin, and B. L. Turner. 1994. The Global Impact of Land-Use Change. Bioscience 44:300-304.

Opdam, P., and D. Wascher. 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117:285-297.

Pascual-Hortal, L., and S. Saura. 2007. Impact of spatial scale on the identification of critical habitat patches for the maintenance of landscape connectivity. Landscape and Urban Planning 83:176-186.

Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. Global Biogeochemical Cycles 13:997-1027.

Red List of Threatened Species, T. I. 1998. Ocotea uxpanapana. World Conservation Monitoring Centre. The IUCN Red List of Threatened Species, www.iucnredlist.org.

Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist 158:87-99.

Saura, S., Ö. Bodin, and M.-J. Fortin. 2014. Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. Journal of Applied Ecology 51:171-182.

Schloss, C. A., T. A. Nunez, and J. J. Lawler. 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences of the United States of America 109:8606-8611.

Schtickzelle, N., and M. Baguette. 2003. Behavioural Responses to Habitat Patch Boundaries Restrict Dispersal and Generate Emigration-Patch Area Relationships in Fragmented Landscapes. Journal of Animal Ecology 72:533-545.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Plant Ecology 107-108:15-29.

Schupp, E. W., P. Jordano, and J. M. Gomez. 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytologist 188:333-353.

Tambosi, L. R., A. C. Martensen, M. C. Ribeiro, and J. P. Metzger. 2014. A Framework to Optimize Biodiversity Restoration Efforts Based on Habitat Amount and Landscape Connectivity. Restoration Ecology 22:169-177.

Terborgh, J., G. Nunez-Iturri, N. C. A. Pitman, F. H. C. Valverde, P. Alvarez, V. Swamy, E. G. Pringle, and C. E. T. Paine. 2008. Tree recruitment in an empty forest. Ecology 89:1757-1768.

Turner, I. M., and R. T. Corlett. 1996. The conservation value of small, isolated fragments of lowland tropical rain forest. Trends in Ecology & Evolution 11:330-333.

Uezu, A., D. D. Beyer, and J. P. Metzger. 2008. Can agroforest woodlots work as stepping stones for birds in the Atlantic forest region? Biodiversity and Conservation 17:1907-1922.

Vandermeer, J., and I. Perfecto. 2007. The agricultural matrix and a future paradigms for conservation. Conservation Biology 21:274-277.

Wendt, T., and H. v. d. Werff. 1987. A New Species of Ocotea (Lauraceae) from Southeastern Mexico. Annals of the Missouri Botanical Garden 74:413-415.

Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. Ecology 66:808-818.

5.6 TABLES

Table 5.6.1. Summary of correlations between all evaluated variables and the multiple regression analysis of centered minimum LCP (cost), centered canopy openness (cover) and their interaction. *P<0.05, **P<0.01, ***P<0.001.

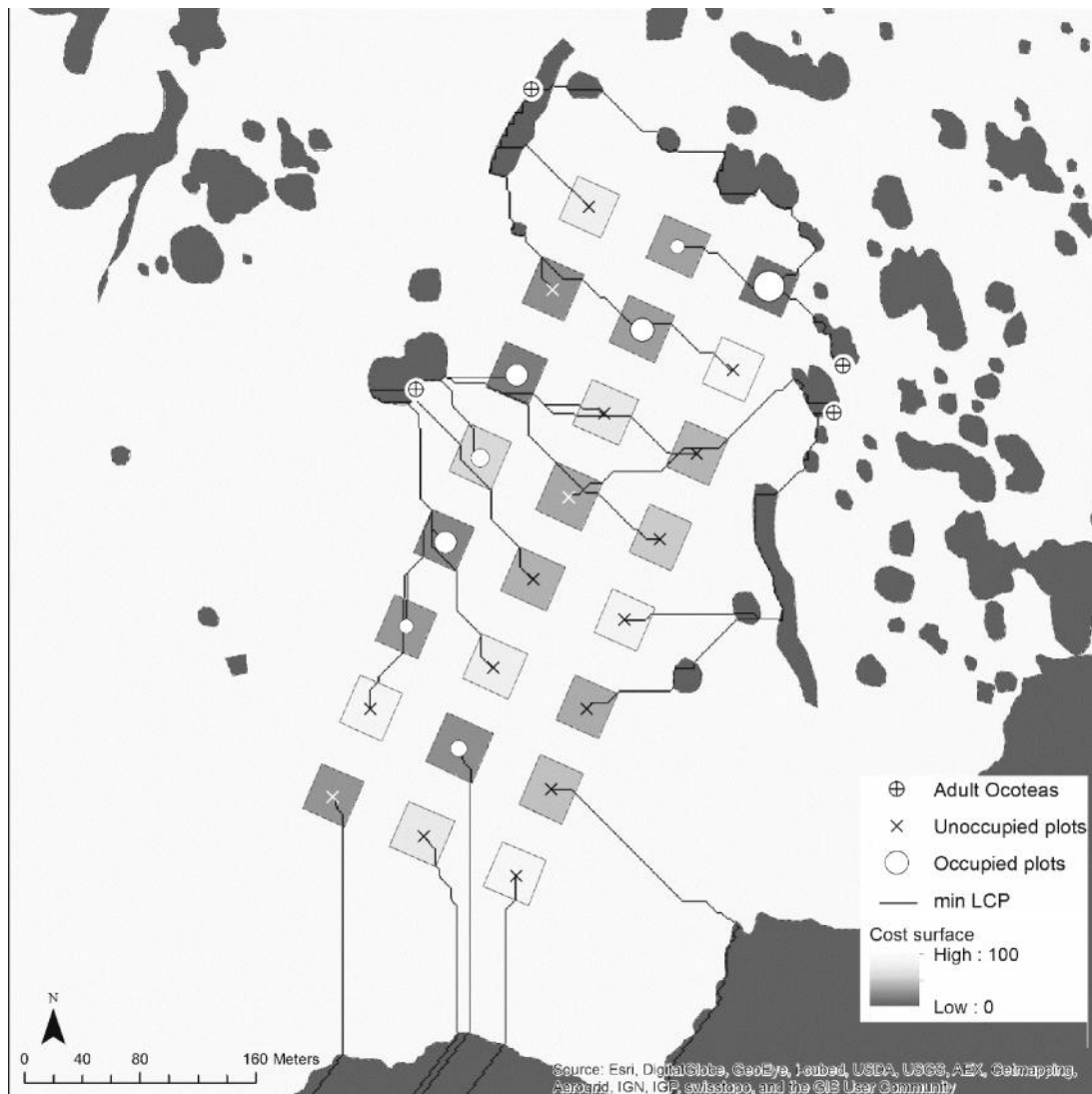|	Ln cost distance	Ln openness	No. Routes	Ln Euclidean distance
Seedlings	-0.617**	-0.661**	0.541*	-0.496*
Ln cost		0.34	-0.529*	0.876***
Ln openness			-0.755***	0.268
No. Routes				-0.457*
	Coefficient	Std. Error	t	p
Constant	1.27	0.39	3.20	0.01
center(cover)	-2.12	0.73	-2.89	0.01
center(cost)	-1.99	0.79	-2.52	0.05
interaction	2.87	0.96	2.97	0.01
	DF	SS	F	p
Regression	3	191.29	18.08	<0.001
Residual	20	70.55		
Total	23	261.83		

Figure 5.7.1. Site maps presenting cost surface values after restoration. Cost values are zero to 100, where zero represents completely forested areas (dark gray) and 100 are completely open areas (light gray). Destination plots are crossed white circles and the least cost paths from a potential *Ocotea* parent tree to each plot and presents with black lines. Unoccupied plots are shown with an ex, occupied plots are represented with a white circle and its size represents the abundance of *Ocotea* seedlings.
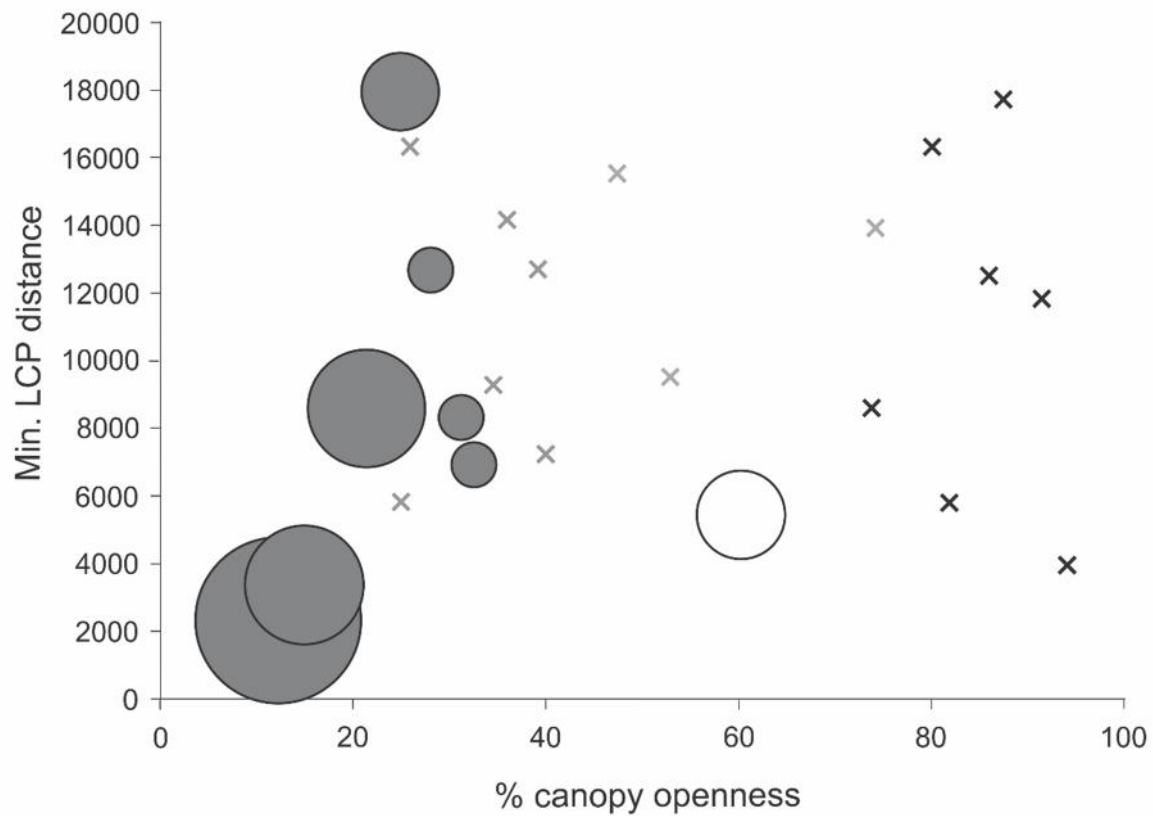
Figure 5.7.2. Distribution of canopy openness and cost path distance across experimental restoration plots in relation to the establishment of Ocotea seedlings. The size of the circles is related to *Ocotea* seedling abundance. Gray circles are planted plots (with animal- or wind-dispersed tree species) and open circles are unplanted controls. Gray crosses are unoccupied planted plots and black crosses are unoccupied control plots.
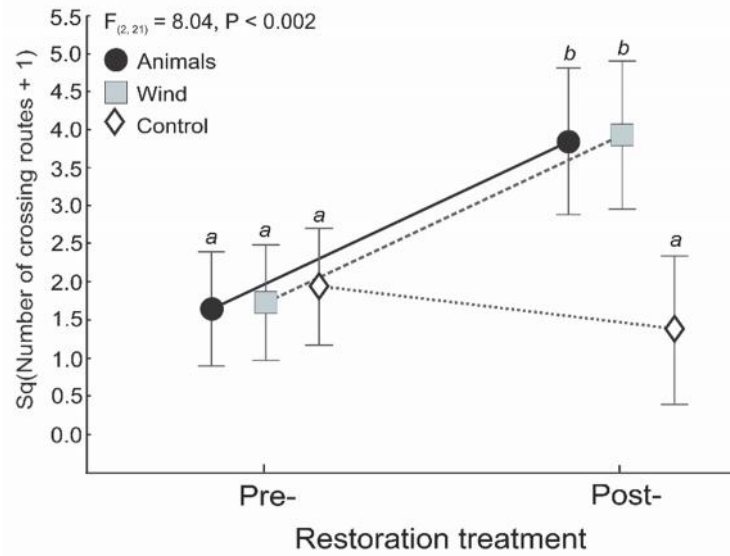
Figure 5.7.3. Number of crossing routes by restoration treatment in pre- and post-restoration treatment. Means are represented by black circles (animal-dispersed plantings), grey squares (wind-dispersed plantings), and white diamonds (controls). Error bars indicate 95% confidence intervals. Different letters indicate differences based on a Tukey test, $P < 0.05$.

GENERAL CONCLUSIONS

Several factors limit pasture succession back to forest. Dispersal and establishment limitations play a crucial role in assembly of species in successional vegetation. In the competition for space, reaching a new site is critical. However, it is also important to consider sheer numbers; how many seeds are reaching this new site? How many recruits actually establish? How many seeds are needed to produce at least one recruit? What are the odds in the early stages of a plant to make it to a mature age given intraspecific competition and heterospecific seeds arriving? Some of these questions can be answered through dispersal and establishment limitation indices, which can give a preliminary picture of the early dynamics that occur in regeneration and succession of plant communities in different habitat types.

Primary and secondary forest showed different dynamics of dispersed seeds and established recruits, yet in pastures, limitations were more severe than in both forest types. Few seeds actually made it into pastures away from the forest edge, but even fewer resulted in established recruits. Species with low dispersal limitation were often more establishment -limited and vice versa, indicating a trade-off between fecundity and tolerance of seeds survival and establishment. Categories of life histories and dispersal modes are useful in untangling the different traits that explained the tolerantce-fecundity trade-off. In general, later successional species seemed to be more tolerant than fecund, and vice versa for all pioneer species. Seeds of pioneer wind-dispersed trees predominated in secondary forests and pastures, but most established seedlings in all habitats were animal-dispersed pioneer and later successional species. In recently abandoned pastures,

mainly small wind-dispersed seeds of pioneer species arrive, but these rarely manage to establish as seedlings. In contrast, animal-dispersed seeds establish in greater amounts but seeds arrive in very low numbers.

We tested the effect of mixed-species plantings on the acceleration of natural succession. Seedling recruitment increased greatly under mixed tree plantings of wind-dispersed and animal-dispersed species within the first five years of cattle exclusion and planting establishment compared to control plots that were just cattle excluded. As plantings developed larger canopies, more animals were attracted to the plots, which increased the seed arrival for species with higher establishment rates. The wind-dispersed pioneer *Heliocarpus appendiculatus* played an important role in the initial acceleration of succession in planted plots. With a fast growth rate and a wide canopy that 1) suppressed the grass allowing recruited and 2) produced high amounts of litter and primary productivity (reviewed in, Esquivel-Valencia 2012).

Dispersal events into stepping-stones are likely to be mediated by wind or flying animals because many terrestrial animals normally avoid crossing open pastures. Frugivorous bats and birds are known to contribute to forest succession through seed dispersal. Bats mostly defecate in flight; seeds are dispersed scattered throughout the landscape. When seeds land in open and active pastures, seedlings are unlikely to survive trampling and foraging by livestock. On the other hand, birds defecate most larger seeds when perched, thus most of the seeds will fall under trees or, in this case, in planted fenced plots. Seeds that fall under trees have an advantage because the micro environmental conditions favor their establishment and survival (Slocum 2001). This is especially true for seedlings of later successional trees.

On a landscape level, how effective are mixed-species plantings in providing functional

connectivity for forest trees? Can they assist conservation of local biodiversity? For the

large-seeded vulnerable endemic *Ocotes uxpanapana* tree, planted plots proved to be

effective at recovering. Dispersal costs from potential parent trees into planted plots were

reduced, especially to planted plots that were occupied by the species. Dispersal vectors

of *Ocotea*, like toucans and oropendolas, were effective in bringing seeds from the forest

into vegetation patches that provided ideal establishment conditions. The increase in

canopy cover was also a factor that promoted the recruitment of seedlings of this forest

tree species.

Management recommendations

1. Cattle exclusion is the first factor that will allow succession to initiate. Seeds that
    fall in open active pastures and survive desiccation and high levels of seed
    predation are often trampled or eaten by cows as seedlings.

2. Plant trees that provide shade early and suppress grass to allow seedling
    establishment. For example, fast-growing pioneer *Heliocarpus appendiculatus* trees
    produce enough shade to suppress grasses and allow seedling establishment (de la
    Peña-Domene et al. 2013). The tree also produces high amounts of leaf litter
    (Esquivel-Valencia 2012), providing organic matter which then increases soil
    fertility and helps maintain soil humidity (Bryan 1999).

3. Planting trees that provide fleshy fruits attractive to animal dispersers increases
    disperser visitation and seed dispersal from nearby forest patches (Figure 6.1)

4. Higher planting densities and richness will help to attract a larger cohort of seed disperser and thereby a higher number of dispersed trees.

5. What is in it for cattle ranchers? Plantings of fruit-bearing trees can also be of economic importance for local cattle ranchers. Some of these trees rapidly produce fleshy fruits edible for humans.

6. Loss of native habitat also affects agricultural production by degrading ecosystem services that are important for agriculture (e.g. pollination, soil fertility and water regulation; Foley et al. 2005). Tree patches provide ecosystem services that have indirect effects on cattle production, such as maintaining and improving soil fertility (Bryant et al. 1997, Bryan 1999), increasing organic matter, recycling nutrients and countering soil compaction, and reducing surface runoff and erosion (Ilstedt et al. 2007). Integrating trees as part of the productive system promotes inter-fragment migration of many organisms (Vandermeer and Perfecto 2007), including bird and insect predators and parasitoids that control harmful insects in pastures (Murgueitio et al. 2011).

7. Cattle ranchers may overlook benefits provided by trees in pastures. Engaging the local community through informal talks and workshops will achieve maximum participation. If more cattle ranchers are willing to change their conventional grazing pastures to low environmental impact strategies, a higher scale of conservation of tropical rainforest species can be achieved.

8. Comparative studies in the Neotropics have shown that silvopastoral systems (agroforestry arrangements that combine grasses with shrubs and trees for animal

nutrition and complementary uses) may reach production levels equal to or higher than conventional grazing systems. Vegetation patches can potentially also extend pasture lifespan though the maintenance of soil fertility (Jones and Bunch 1995). "Cattle ranching does not have to be the cause of serious environmental problems. Instead, it may be part of the solution … applying the available practical knowledge on the uses and benefits of trees" (reviewed in Murgueitio et al. 2011).

9. In silvopastoral systems, cattle production also reduces the production costs because many ecosystem services are regained and because it can be a self-sustained system (Cuartas Cardona et al. 2014).

10. Combining silvopastoral systems as the matrix of fruit-bearing planted patches may assist in improving the livelihoods of small-scale cattle ranchers in the tropics as well as maintaining landscape connectivity, maintaining ecosystem services and conserving animal and plant species from the tropical rain forest.

11. Combining permeable matrices with high commercial productivity can help create an integrated landscape that will reduce deforestation pleasure and help decrease the effects of fragmentation on local biodiversity.
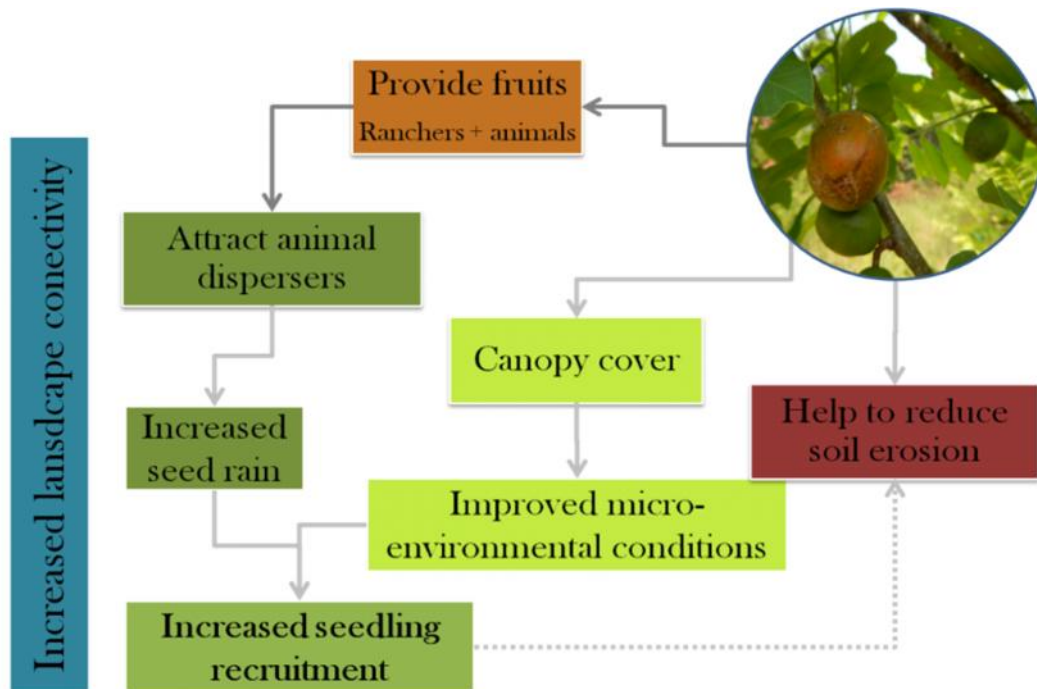
Figure 6.1. Diagram of the succession process and its effects on ecosystem services

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LITERATURE CITED

Bryan, J. 1999. Nitrogen fixation of leguminous trees in traditional and modern agroforestry system. Pages 165-186 *in* M. S. Ashton and F. Montagnini, editors. The Silvicultural Basis for Agroforestry Systems. CRC Press, Boca Ratón, FL.

Bryant, D., D. Nielsen, L. Tangley, N. Sizer, M. Mirand, P. Brown, N. Johnson, A. Malk, and K. Miller. 1997. The last frontier forests: ecosystems and economies on the edge. What is the status of the world's remaining large, natural forest ecosystems? Forest Frontiers Initiative, Washington, D.C.

Cuartas Cardona, C. A., J. F. Naranjo Ramírez, A. M. Tarazona Morales, E. Murgueitio Restrepo, J. D. Chará Orozco, J. Ku Vera, F. J. Solorio Sánchez, M. X. Flores Estrada, B. Solorio Sánchez, and R. Barahona Rosales. 2014. Contribution of intensive silvopastoral systems to animal performance and to adaptation and mitigation of climate change. Revista Colombiana de Ciencias Pecuarias 27.

de la Peña-Domene, M., C. Martínez-Garza, and H. F. Howe. 2013. Early recruitment dynamics in tropical restoration. Ecological Applications 23:1124-1134.

Esquivel-Valencia, I. 2012. Efecto de plantaciones de restauración ecológica experimental en la caída de hojarasca en un pastizal tropical lluvioso en Los Tuxtlas, Veracruz. Universidad Autónoma del Estado de Morelos, Morelos, Mexico.

Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, J. H. Helkowski, T. Holloway, E. A. Howard, C. J. Kucharik, C. Monfreda, J. A. Patz, I. C. Prentice, N. Ramankutty, and P. K. Snyder. 2005. Global Consequences of Land Use. Science 309:570-574.

Ilstedt, U., A. Malmer, E. Verbeeten, and D. Murdiyarso. 2007. The effect of afforestation on water infiltration in the tropics: A systematic review and meta-analysis. Forest Ecology and Management 251:45-51.

Jones, R. M., and G. A. Bunch. 1995. Long-term records of legume persistence and animal production from pastures based on safari Kenya cloves and *Leucaena* in subtropical coastal Queensland. Tropical Grasslands 29:74-80.

Murgueitio, E., Z. Calle, F. Uribe, A. Calle, and B. Solorio. 2011. Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. Forest Ecology and Management 261:1654-1663.

Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology 82:2547-2559.

Vandermeer, J., and I. Perfecto. 2007. The Agricultural Matrix and a Future Paradigm for Conservation. Conservation Biology 21:274-277.

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De la Peña-Domene, M.; Howe, H. F. and Minor, E. Conservation of local biodiversity though increased connectivity in agricultural landscapes, the case of *Ocotea uxpanapana* an endemic vulnerable tree. *In preparation*

De la Peña-Domene, M., Martínez-Garza, C., Palmas-Pérez, S. Rivas-Alonso, E. & Howe, H. F. Birds and bats play different roles in tropical forest restoration. *In press* PlosOne

De la Peña-Domene, M., Cruz-León, E., Urincho-Pantaleón, Y., Jiménez-Rolland, R., Lozano-Huerta,   C., & Martínez-Garza, C. (2012a) Tropical seed potential or realized effectiveness? *Submitted.*

De la Peña-Domene, M. and Minor, E. S, Landscape Connectivity and Ecological Effects, Encyclopedia of Natural Resources, *In proofs*

De la Peña-Domene, M., Martínez-Garza, C. & Howe, H. F. 2013. Early recruitment dynamics in tropical restoration. Ecological Applications. Vol. 23, Issue 5 Pp. 1124–1134

Howe, H.F., Urincho-Pantaleón, Y., de la Peña-Domene, M., Martinez-Garza, C., 2010. Early seed fall and seedling emergence: precursors to tropical restoration. Oecologia 164, 731-740.

Martinez-Garza, C. Flores-Palacios, A. <u>De La Peña-Domene, M</u>. Howe, H. F. 2009. Seed rain in a tropical agricultural landscape. Journal of Tropical Ecology. Vol 25. Pp. 541-550

Orozco-Lugo, C.L.;Valenzuela-Galván, D.; Vázquez L.B.; Rhodes, A.J.; de León-Ibarra, A.; Hernández, A., Copa-Alvaro,M.E.; Avila-Torres Agatón L.J., and <u>de la Peña-Domene, M</u>. 2008. Velvety fruit-eating bat (*Enchistenes hartii; PHYLLOSTOMIDAE*) In Morelos, Mexico. The Southwestern Naturalist, 53(4):517–520

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2011- Chancellor's Supplemental Research Fellowship UIC: Overcoming Barriers to Rain Forest Regeneration in a Mexican Agricultural Mosaic ($4,000 US).

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	ATBC and OTS 50th meeting, San José, Costa Rica
	CLP Learning exchange program: January to February, Juruá and Fortaleza, Brazil
2011	III Mexican meeting of Ecology, E. Rivas Alonso, M. de la Peña- Domene and C. Martínez-Garza. Differential contribution of bird and bats to recruitment in a tropical pasture under different restoration treatments
2009	94 ESA Annual Meeting. M. De la Peña, Y. Urincho-Pantaleon, C. Martinez-Garza Seed and seedling dynamics in three habitats in the tropical rain forest of Los Tuxtlas, Mexico. Albuquerque, USA
2008	II Mexican meeting of Ecology, M. de la Peña Domene and C. Martínez Garza. Seedling recruitment under experimental plantations in tropical pastures
	93 ESA Annual Meeting. M. de la Peña-Domene, C. Martinez-Garza y H. F. Howe. Seedling recruitment in experimental plantations in Los Tuxtlas, Veracruz, Mexico: Effects of the dispersal syndrome of the planted species. Milwaukee, USA
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