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Restored connectivity facilitates recruitment by an endemic large-seeded tree in a fragmented tropical landscape

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Abstract. Many large-seeded Neotropical trees depend on a limited guild of animals for seed dispersal. Fragmented landscapes reduce animal abundance and movement, limiting seed dispersal between distant forest remnants. In 2006, experimental plantings were established in pasture to determine whether plantings enhance seed dispersal and, ultimately, seedling

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recruitment. We examined patterns of naturally-recruited seedlings of *Ocotea uxpanapana*, a large-seeded bird-dispersed tree endemic to southern Mexico that occurs in the surrounding landscape. We used GIS and least-cost path analysis to ask: (1) Do restoration efforts alter recruitment patterns? (2) What is the importance of canopy cover and likely dispersal pathways to establishment? Patterns of seedling establishment indicated that dispersal agents crossed open pastures to wooded plots. Recruitment was greatest under woody canopies. Also, by reducing movement cost or risk for seed dispersers, wooded canopies increased influx of large, animal-dispersed seeds, thereby restoring a degree of functional connectivity to the landscape. Together, canopy openness and path distance from potential parent trees in the surrounding landscape explained 73% of the variance in *O. uxpanapana* seedling distribution. Preliminary results suggest that strategic fenced plantings in pastures increase dispersal and establishment of large-seeded trees, thereby accelerating forest succession in restorations and contributing to greater connectivity among forest fragments.

Key words: experimental restoration, habitat fragmentation, large-seeded trees, least-cost paths, Mexico, stepping-stones, seed dispersal, tropical rainforest

INTRODUCTION

Vast expanses of Neotropical rainforest have been converted to cattle pasture and crops, leaving small forest fragments scattered among farms and pastures (e.g. Montagnini and Jordan 2005). In these fragmented landscapes, persistence of many species depends on their ability to re-colonize or move through habitat patches or take advantage of secondary vegetation (Gustafson and Gardner 1996, Damschen et al. 2008, Chazdon 2014). Maintaining landscape connectivity with corridors or stepping stones is an important option for conservation in the face

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of habitat loss (Heller and Zavaleta 2009). These networks of connected patches potentially counterbalance effects of fragmentation by broadening species distributions and rescuing genetically isolated populations (Alagador et al. 2012, McConkey et al. 2012). Landscape connectivity restored with strategic plantings may also increase the success of conservation efforts (Chazdon 2008, Tambosi et al. 2014), but little empirical work tests the idea.

Most Neotropical rainforest trees and shrubs are dispersed by animals (Jordano 1995). Large-seeded trees are especially vulnerable to fragmentation because they are dispersed by large animals that are less common and are more susceptible to hunting (Markl et al. 2012). In Central American forests, toucans (*Ramphastos sulfuratus* and *R. swainsonii*) range widely while foraging for large-seeded fruits, with frequent seed-dispersal distances of 150-250 m or more (e.g. Kays et al. 2011). However, few large-seeded trees are dispersed by animals into active pastures (Martínez-Garza et al. 2009, Saavedra et al. 2015). An open question is whether toucans or other large birds can effectively and predictably disperse large seeds into experimental plantings in agricultural landscapes.

Experimental plots were established in Veracruz, Mexico in 2006 to determine whether dispersal processes could be manipulated to accelerate succession. Previous work demonstrated that planted plots recruited far more trees and shrubs than controls (de la Peña-Domene et al. 2013). In particular, recruitment of bird-dispersed, primary-forest tree species increased dramatically as planted pioneer trees began to fruit (de la Peña-Domene et al. 2014).

To determine whether different restoration treatments affect recruitment in predictable ways, we assess recruitment patterns directly rather than examine seed rain (de la Peña-Domene et al. 2013, 2014). Dispersal is a necessary precondition for recruitment, but so many density-dependent and density-independent factors intervene between the seed and sapling stages that

patterns of seed fall are barely reflected in effective recruitment (e.g. Harms et al. 2000, Howe et al. 2010, Schupp et al. 2010, Caughlin et al. 2015). This is particularly the case in heavily disturbed habitats where seed sources are far from recruitment sites.

Here we used a spatially-explicit approach to examine patterns of recruitment of large-seeded *Ocotea uxpanapana* (Lauraceae), a vulnerable tree (WCMC 1998) endemic to southern Mexico. We hypothesized that planted plots shaped recruitment patterns of this species, first by attracting large birds to fruiting trees and cover, and second by providing shaded conditions suitable for seedling establishment and growth.

METHODS

Study site and species

The 640 ha Los Tuxtlas Biological Station (LTBS) lies in the northern portion of the 155,000+ ha Los Tuxtlas Biosphere Reserve in Veracruz, southeast Mexico. The landscape in the reserve is highly fragmented, but LTBS is part of a large fragment (~9,000 ha) of tropical rain forest with ~35 m high closed canopy. Mean annual temperature and rainfall are 27° C and 4,900 mm, respectively (González-Soriano et al. 1997). Our site is a 12 ha pasture that has been intensively grazed by cattle for 30-40 y, embedded in a mosaic of farms, isolated trees, and primary and secondary forest.

Ocotea Aubl. is a genus of > 300 recognized species of trees and shrubs, mostly in the Neotropics (Van der Werff 2002). *Ocotea uxpanapana* is a recently-described tree growing to 30 m and up to 1 m dbh (Wendt and van der Werff 1987). The species has distinctive narrow leaves to 25 cm long and green ellipsoid fruits 22 mm long to 19 mm wide. The seed is dark brown and ~ 20 mm long x 18 mm wide. It is endemic to mature rainforests of southern Veracruz (Arroyo-Rodríguez et al. 2009). It also occurs as a relic tree in wooded pastures.

Experimental design

In July - August 2006, 24 fenced plots (30 x 30 m) each separated by 35 m of active dairy pasture (central GPS 18° 35' 43.64" N, 95° 06' 06.29" W) were established adjacent to privately-owned late secondary forest continuous with LTBS (Fig. 1, S2). The SE corner of the grid was 95 m from late secondary forest, which was continuous with the edge of LTBS 714 m away. Individually tagged seedlings of 24 tropical tree species from 15 families were planted in in 2006 and 2007 (Martínez-Garza et al. 2013). Eight plots were planted with seedlings of animal-dispersed species (none Lauraceae), eight with seedlings of wind-dispersed species, and eight were left as unplanted controls to simulate natural succession. Distribution of treatments among the plots was selected at random. Broad characteristics of seed rain were assessed in the plots from 2007 to 2011 and again from 2013 to 2014. Of 369,493 seeds, 92% were small and wind-dispersed (45% were *Eupatorium pycnocephalum*). Average seed rain was 3,225 seeds month⁻¹ in 2007 and increased to 30,276 seeds month⁻¹ in 2014. A few seeds, belonging to 66 species, exceeded 15 mm in width; none were *Ocotea* (Popoca, in preparation). Sampling effort for seed rain (< 1% of the area sampled for recruitment) detects broad patterns but not rare species.

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 seed traps and 0.5 m² spaces for planted seedlings in planted plots. Total sampled area was 14,415 m² over a period of seven years. Seedlings > 10 cm high were the smallest size that could reliably be found. The present study reports recruited seedlings from 2011, when the species was first documented, to January 2014. In the last census, 38 individuals represented the entire population of recruited *O. uxpanapana* in the plots; recruits ranged from 14-83 cm tall (41 + 19 s.d. cm).

Because *Ocotea* fruits are large and birds were unlikely to carry more than one at one time, we assumed that recruits were from separate dispersal events. We also recorded the location of all reproductive conspecifics (N = 12) in the surrounding 100 ha.

Canopy cover and seedling recruitment

Canopy may affect *O. uxpanapana* recruitment in two ways. First, woody vegetation indirectly affects seed dispersal by providing cover and food for forest birds. We examine this indirect effect with least-cost path analysis of established seedlings to determine whether they reflect random patterns with respect to mature conspecifics and the patchwork of experimental stands of trees. Second, by suppressing grasses and ferns, canopy cover benefits *O. uxpanapana* establishment. To tease apart these effects, we measured canopy cover in plots and mapped distances to reproductive conspecific trees in the surrounding landscape. In July 2012 we took 12 high-contrast canopy photos per plot, subtracted the non-luminous pixels in each photo from total pixels, and calculated the mean % openness per plot. For the remaining landscape (outside the plots), we used ArcMap 10.1 to digitize individual trees and surrounding forest from a 2009 aerial photograph, with conversion to a binary raster data layer of 1 m resolution.

We estimated probability of effective seed dispersal (i.e. dispersal resulting in seedlings, Schupp et al. 2010) into each plot based on a set of distance measures from potential parent trees. 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. Free, open-source alternatives to ArcMap include Geographic Resources Analysis Support System (GRASS) and System for Automated Geoscientific Analyses (SAGA).

The cost path tool found the path from point A (each reproductive adult) to point B (each study plot) that accumulated the minimum total cost. Accumulated cost reflected the difficulty

associated with traversing different parts of a landscape for the disperser. Higher costs represented species-specific factors that plausibly impeded movement, such as energetic cost or exposure to predation risk (Etherington and Holland 2013). The path was based on a resistance or “cost” surface that a bird might incur while crossing the landscape. Because *O. uxpapanana* was primarily dispersed by large forest birds, we assumed that increased canopy cover would generate lower costs for the birds (higher potential rewards of food and lower perceived risk), leading to lower dispersal costs for the plant. The cost surface assigned a value of $(100 - X\%$ canopy cover) to each 1m^2 pixel, where X represented the canopy cover in that pixel. These paths could wind across the landscape in non-linear ways, influenced by the presence of isolated trees, small forest patches and living fences (Fig.1). Once Euclidean distances and LCPs were calculated from all reproductive adults, we identified the minimum Euclidean distance and the minimum LCP for each plot. These minimum values represented distance to the nearest reproductive adult and were used in our models as estimates of seed-dispersal probability.

As a third estimate of seed movement probability, we counted the number of times a LCP passed through each plot *en route* to other plots. LCPs, and the number of times a path crossed through each plot, were calculated before restoration (no woody canopy) and after restoration, allowing examination of how restoration might alter dispersal paths across the landscape.

Recruits did not establish in active pasture surrounding plots. Cattle ate woody species emerging in active pasture except *Conostegia xalapensis* (Melastomaceae) and *Stemmadenia donnell-smithii* (Apocynaceae), which are eradicated by the landowner.

Statistical analysis

We used correlation to examine relationships between seedling abundance in each plot, canopy cover in the plot, and dispersal probability. Relationships among canopy cover, minimum

Euclidean distance, and minimum least cost distance were non-linear; those variables were natural-log transformed. We used multiple linear regression to evaluate the combined importance of local canopy cover, seed dispersal probability, and their interaction term on *O. uxpanapana* establishment, a procedure less prone to type I errors than generalized linear models (Ives 2015). We included the dispersal probability variable that most strongly correlated with number of *O. uxpanapana* seedlings in the model. Canopy cover and dispersal probability were natural-log transformed and then centered before calculating the interaction term to reduce collinearity and increase interpretability of regression slopes. To address questions about the effect of restoration on seed dispersal routes, we used repeated measures ANOVA with number of crossing routes as a dependent variable and experimental treatment (control and plantings of wind-dispersed or animal-dispersed species) and time (before or after restoration) as independent variables. We used Statistica 7 and R for all statistical analysis.

RESULTS

The number of *O. uxpanapana* seedlings increased as a function of the number of crossing routes through each plot and decreased as a function of Euclidean distance, LCP distance, and canopy openness (Table 1). Predictor variables were significantly correlated with number of *O. uxpanapana* seedlings. Because LCP distance was the most strongly correlated dispersal-probability variable, it 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 2). A “best subsets regression” approach, which tests all combinations of predictor variables, indicated that the best model ($\Delta\text{AICc} > 4$) included all predictor variables (data not shown). Together, these three variables explained 73% (adjusted $r^2 = 0.69$) of the variability in number of seedlings of this species per plot. *Ocotea uxpanapana* seedlings rarely

established with more than 35% canopy openness (Figure 2a, Table S1). Seedling abundance was highest in plots with low canopy openness and short LCP distances.

Prior to restoration, treatments did not differ in number of indirect routes crossing plots *en route* from potential parent trees to destination plots (mean 3 ± 5 SD routes per plot). After 7 years of growth and establishment, planted plots significantly increased in number of indirect routes compared to unplanted control ($F_{(2, 21)} = 8.04$, $P < 0.005$, Fig. 2b). Plots planted with wind-dispersed trees increased from 2.5 ± 3.1 to 18 ± 15 routes plot⁻¹; plots planted with animal-dispersed trees increased from 2.1 ± 2.9 to 14.4 ± 6.3 routes plot⁻¹. Number of *O. uxpanapana* seedlings also increased with number of dispersal routes crossing plots ($r = 0.54$, $P < 0.005$).

DISCUSSION

We show that small plots of planted trees can serve two important functions in conservation and restoration in a largely deforested tropical landscape. Recruitment suggests that canopy cover in these plots creates a suitable environment for establishment of later-successional tree species; *Ocotea* rarely establishes when canopy cover is less than 65%. Moreover, by altering dispersal pathways of agents of seed dispersal, canopy cover in plots increases influx of large, animal-dispersed seeds and restores a degree of functional connectivity to the landscape. Small pre-existing patches also play an important role in this landscape (Fig. 1). An anomaly in our data provides further support for this idea: four *Ocotea* seedlings were found in a control plot with a fairly open canopy (60% openness), but this plot was directly adjacent to a small stand of trees that included an adult *Ocotea* (Fig. 1). A growing literature indicates a need to increase connectivity by facilitating seed dispersal; we offer a preliminary experimental demonstration towards proof of concept.

Small vegetation patches can act as stepping-stones that increase animal movement through fragmented landscapes. The spatial arrangement and quality of habitat patches significantly affect the rate of animal movement through them (Collingham and Huntley 2000, Tambosi et al. 2014). In our case, toucans and oropendolas frequently forage in isolated fruiting shade trees and in our small experimental plots (unpublished data); they appear to be efficient dispersers for *Ocotea* and other large-seeded species. Toucans largely frequent forests, but also range widely over isolated fruiting trees, fragments, living fences and riparian strips (Guevara and Laborde 1993, Slocum and Horvitz 2000). In the Yucatan Peninsula of Mexico, toucans frequent forest patches larger than 22 ha, but not small patches of 2 - 3 ha (Melo et al. 2010). Different results at Los Tuxtlas are likely due to patch quality rather than patch size. Our planted patches offer food resources and shelter that are attractive to large fruit-eating birds. At Los Tuxtlas, Graham (2001) finds that presence of these toucans in forest fragments is correlated with food abundance rather than fragment size. An approach that specifically restores habitat and functional connectivity for avian dispersers of large seeds is promising.

Of three measures of dispersal probability, abundance of *O. uxpanapana* seedlings was most strongly correlated with LCP distance from mature conspecific trees. Euclidian distance was also correlated with seedling establishment but this metric ignored ecological cost of movement for seed dispersers. Accumulated costs in LCPs better described the difficulty or perceived risk associated with traversing different parts of a landscape (Etherington and Holland 2013). Euclidian distances from potential parent trees to restoration plots were invariant, while least cost paths changed with restoration. Changed movement paths are indicated by the increased number of crossing routes through planted plots (Fig. 2B). Although vegetation cover in the control plots also increased over the course of the study, the relative attractiveness of these

plots (with respect to experimental plots) decreased, and thus the number of crossing routes through control plots did not change.

Our assessments of effective dispersal using established *O. uxpanapana* seedlings likely underestimated the spatial extent of seed movement (see Kamm et al. 2010, Schupp et al. 2010). Nonetheless, the patterns of actual recruitment from dispersed seeds indicate the importance of enriched forest plantings in active agricultural landscapes. Our results likely apply to other large-seeded tree species facing similar dispersal constraints, some of which (e.g. *Nectandra ambigens*, *Virola guatemalensis*, *Pseudolmedia oxyphyllaria*) have also colonized our experimental plantings from nearby forest (de la Peña-Domene et al. 2014).

With widespread conversion of forest to agriculture and increasing fragmentation, the ability of tree species to move is critical (Corlett and Westcott 2013). For most tropical trees and shrubs, this requires heterogeneous landscapes that support animal populations, permit temporary breeding populations of plants, and facilitate animal and plant migration. Our approach is to create heterogeneous matrices between remnants that allow persistence and movement of tree species that are capable of coexisting with agrarian economies (e.g. Perfecto and Vandermeer 2010). The capacity of species to exploit opportunities created by networks of stepping-stone patches is, to a degree, species-specific. Species not disseminated by mobile animals are unlikely to colonize small, isolated forest patches or traverse forbidding landscapes. For those capable of movement assisted by habitat islands, strategic restoration offers a potential for maintenance of metapopulation dynamics in the short term and pathways for range shifts in the long term.

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DESCRIPTION OF SUPPORTING INFORMATION

Table S1: Planting treatments and number of seedlings in each plot.

Figure S2: Enlarged view of the study area and surrounding landscape

Table 1. Summary of correlations between all evaluated variables.

	<i>ln(openness)</i>	<i>ln(cost distance)</i>	<i>No.Routes</i>	<i>Ln Euclidean distance</i>
<i>Seedlings</i>	-0.661**	-0.617**	0.541*	-0.496*
<i>ln(openness)</i>		0.34	-0.755***	0.268
<i>ln(cost distance)</i>			-0.529*	0.876***
<i>No.Routes</i>				-0.457*

*P < 0.05, ** P < 0.01, *** P < 0.001.

Table 2. Multiple regression results explaining number of *Ocotea* seedlings in each plot. Canopy cover and least cost path distance (LCP) were natural-log transformed and centered before analysis. Model $r^2 = 0.73$.

	<i>Coefficient</i>	<i>Std. Error</i>	<i>t</i>	<i>P</i>
Constant	1.27	0.39	3.20	0.01
Canopy cover	-2.12	0.73	-2.89	0.01
LCP	-1.99	0.79	-2.52	0.05
interaction	2.87	0.96	2.97	0.01
	<i>DF</i>	<i>SS</i>	<i>F</i>	<i>P</i>
Regression	3	191.29	18.08	<0.001
Residual	20	70.55		
Total	23	261.83		

Accepted Article

Figure 1. Close-up of the site map of 24 experimental restoration plots embedded in pasture. Areas to the south and west of the plots are largely covered by tropical rain forest. Cost surface values shown after restoration range from zero to 100, where zero represents completely forested areas (dark gray) and 100 are completely open areas (light gray). Unoccupied plots are shown with an x and occupied plots are represented with a white circle, with size representing the abundance of *O. uxpanapana* seedlings. Planting treatments are indicated by letters: A for plantings of animal-dispersed trees, W for plantings of wind-dispersed trees and C for unplanted control plots. Mature *Ocotea uxpanapana* trees are crossed white circles and the black lines show some least cost paths from a potential conspecific parent tree to each plot. Not all potential parent trees in the surrounding 100 ha are shown in the map. A larger spatial extent, with more potential parent trees, is shown in Figure S2.

Figure 2. (A) Canopy openness and cost path distance in relation to the establishment of *Ocotea uxpanapana* seedlings. Circles indicate plots in which *O. uxpanapana* established. Black circles are plots with animal-dispersed plantings, gray circles are plots with wind-dispersed plantings, and open circles are unplanted controls (color key is the same in A and B). The least cost path (y-axis) is unitless. (B) Relation of crossing paths and treatments through time. Number of crossing routes by restoration treatment in pre- and post-restoration. 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, $P < 0.05$.

Figure 1

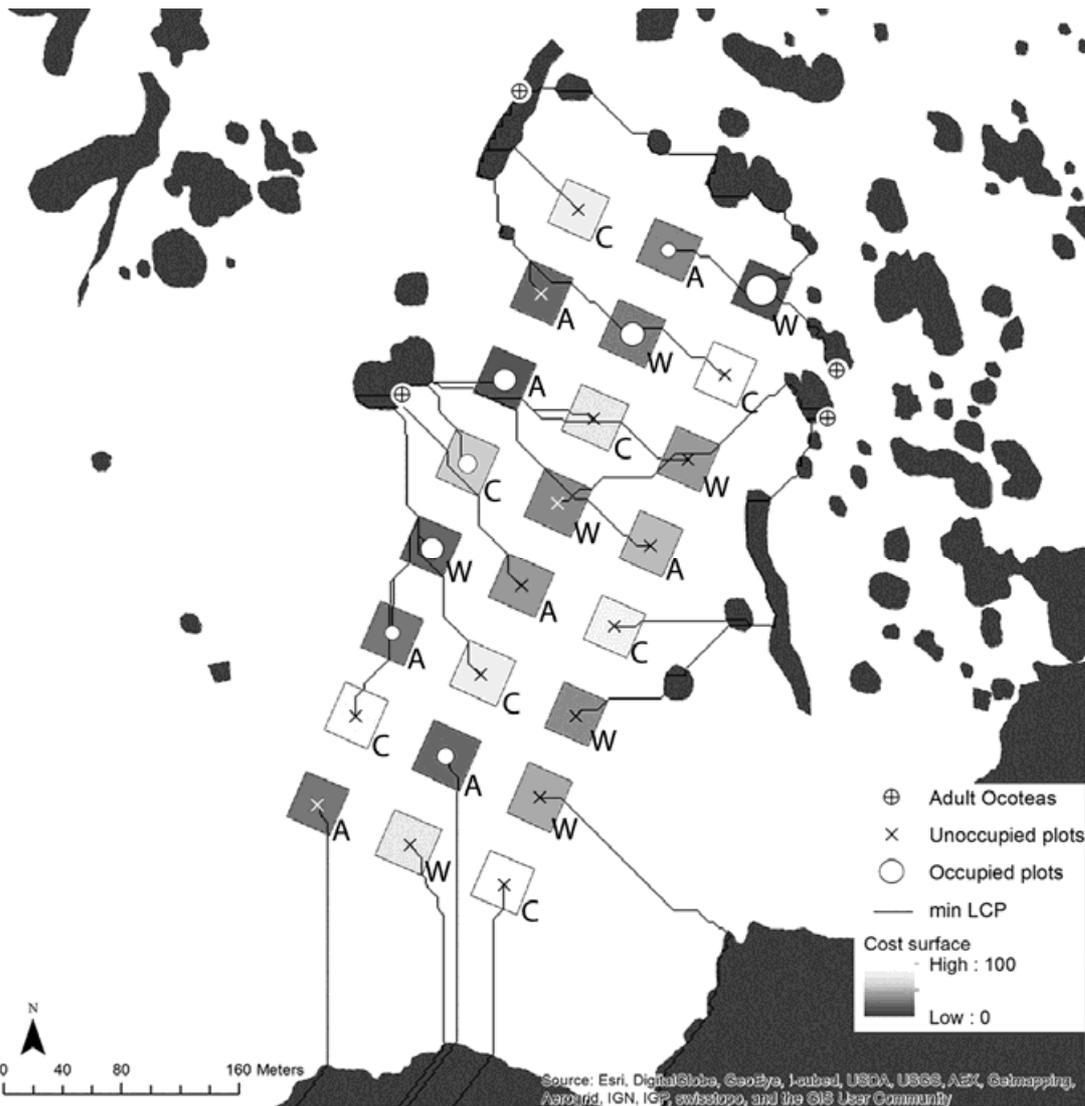


Figure 2

