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Breaking Barriers of Regeneration: Examining the Effectiveness of Bird Perches in Facilitating Seed Dispersal in a Tropical Dry Forest

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Thesis Submitted to the Graduate School at the University of Missouri – St. Louis in Partial Fulfillment of the Requirements for the Degree of Master in Science in Biology

August, 2007

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Abstract

This project examined the use of bird perches in facilitating seed dispersal to address the lack of seed dispersal and seed rain in degraded tropical forests. The goal of this project was to learn more about this practice in order to derive more realistic expectations of its effectiveness. After four months, significantly more seeds were dispersed into plots containing introduced perches as compared to subplots that lacked perches. Seed rain was dominated by Ficus citrifolia, a mid-level successional species, indicating that introduced artificial perches may influence the regeneration of more mature forests. Seeds recovered from seed traps represented species with close proximity to the plots. Seeds dispersed beneath perches were correlated positively with those occurring in surrounding forests. There were eight bird species recorded utilizing perches. Birds species found utilizing perches were also positively correlated with those found within surrounding forest. These results suggest that bird perches in tropical forests may have a very local effect in that species dispersed may be limited to those found in close range to perch structures, but that the perches are effective at providing a seed rain of those species.

INTRODUCTION

Conversion and degradation of tropical forests as a result of human activities (e.g., logging, agriculture, ranching) is having huge impacts on forests throughout the world. Many of these practices greatly degrade forests and the soils on which they are based, often to the point where forests do not reestablish (World Resource Institute, 1992). It is projected that within the next few decades, if the rate of deforestation continues, little tropical forest will remain in the world (Myers, 1991). Yet, cutting down forests for resources is an integral part of our society and these practices should be expected to continue. It is imperative, however, that we understand the dynamics that influence forest recovery so we may be able to sustain forest resources over time and minimize biodiversity loss. The endangerment of many species is caused by habitat loss, degradation and isolation of remaining habitat (Pimm and Raven, 2000). In many regions of the world's tropics, maintenance of biodiversity will require restoration of degraded lands. This project aims to provide insight into seed dissemination limitation that inhibit the regrowth of tropical forests, as well as subsequent effective management practices that may combat natural barriers to the regeneration of tropical forests.

Tropical Deforestation

Deforestation of tropical rainforests is a pressing conservation issue. Approximately 4 billion hectares of the world's tropical forests have been converted to other land uses (Food and Agriculture Organization of the U.N., 2003). As tropical deforestation continues, a greater quantity of land area will become secondary forest (Brown and Lugo, 1990). Though much tropical land is converted to pasture, most of this land is abandoned within the first 10 years of cultivation because of soil degradation, invasion of unpalatable grasses, or changing economic incentives (Buschbacher, 1986), in effect abandoning a large percentage of land as degraded forest. Many of the factors that cause farmers to abandon land are the same that hinder the natural regeneration of these forests. The land is then left stripped of mechanisms, such as seed dispersal, that can assist in the return of woody vegetation. Consequently, forest regrowth is slow or, in some cases, unachievable. Forest regrowth following abandonment of agriculture or ranching minimally requires an existing seed bank or new input of seeds from wind or animal vectors. If the land has been used for many years, or has been severely degraded, few seeds persist in the seed bank, especially in lowland humid forests. The opportunities for new seed input depend on whether seed sources are nearby and if animal vectors enter or traverse the regenerating patches (Holl, 2000). The microclimate of degraded tropical lands are often much more harsh with higher temperatures, increased competition with earlier successional species, as well as changes in rain patterns in very large areas of degraded forest. This project experimentally examined a small segment of these limitations to forest regeneration for animal-dispersed plants – seed arrival. The process of seed arrival is centered on seed dispersal, and the interaction of animal dispersers with cleared areas, intact forest, and introduced and naturally occurring tree perches within these disturbed areas (i.e., cleared areas previously covered with forest vegetation).

Birds and Regeneration

Birds are integral seed dispersers in tropical forests and therefore a necessary consideration when examining the dynamics of regeneration. It has been estimated that seeds of 50%-90% of canopy trees have adaptations for animal dispersal (Howe & Smallwood, 1982). Seed dispersal is widely accepted to have profound effects on vegetation structure (Wang et al., 2002). Lack of seed dispersal, specifically in West Indian forests, the origin of many species dispersed to Key Largo, has been identified as a major barrier to tropical forest regeneration (Zimmerman et al., 2000), and the availability of perches is an essential tool in attracting seed dispersers (Wunderle, 1997). If disturbed areas are not structurally accessible to animal dispersers, then the seed bank may represent a vastly reduced portion of the local vegetative biodiversity (Wunderle, 1997; Greenberg, 1999). In restoration, the dispersal of old-growth and canopy species is an important aspect of forest recovery.

There has been limited study regarding the potential role of perches in degraded tropical forests in effectively facilitating seed dispersal (Holl, 1998; Aide and Caelier, 1994; Wunderle, 1997, Shiels, 2003, Zanini and Ganade, 2005). Further, little is known of the characteristics of bird species, including their distribution and relationship to surrounding forests, as understanding this relationship may aid in the effectiveness of placement of perches, as well as their potential effectiveness as a management and forest recovery tool. It is also important to note the successional stage of plant species being dispersed into degraded areas (e.g., mature versus earlier successional plant species), which may indicate the speed at which a forest is likely to recover.

SPECEFIC HYPOTHESES & QUESTIONS

The rate of succession and recovery in disturbed tropical forests depends upon various mechanisms including seed dispersal. The overall objective of this study is to evaluate the effectiveness of perches in relationship to bird dispersers and surrounding forests to promote this mechanism. To meet this objective I addressed the following questions: (1) Are perches an adequate means to increase seed dispersal in disturbed forest in Upper Key Largo, Fl? (2) What are the common traits among plant species (e.g., life form, principal habitat) that are dispersed underneath artificial perches? (2) Is there a difference in bird usage among artificial perches and trees? (4) What bird species are the dispersers, and what is their normal habitat association and diet?

To answer these questions I tested the following hypotheses:

Hypothesis (1): Perches facilitate seed arrival in degraded areas. Specifically, I expected to find that seed rain would be great underneath perches in comparison to control sites without perches. This prediction is based upon previous studies conducted on the effectiveness of perches in facilitating avifaunal seed dispersal into abandoned tropical pastures in which a positive correlation was noted (Holl, 1998; Aide & Cavelier, 1994; Zanini & Ganade, 2005).

Prediction (1): Seeds dispersed will be dominated by mature, later successional species.

Prediction (2): Seed dispersal is expected to be distance-limited and, thus, most seeds that arrive into degraded areas are expected to be representative of adjacent forests, which act as seed sources.

Prediction (3): I hypothesized that the major dispersers would be a non-random subset of local avifauna. More specifically, I expected generalist bird species to be to visit open areas and carry seeds into degraded areas more often than specialists.

Prediction (4): A significant portion of birds recorded using perches will be seed dispersers rather than non-seed dispersers.

METHODS

Site Description

Upper Key Largo, FL

My study was conducted within the Crocodile Lakes National Wildlife Refuge of Upper Key Largo, Florida. The forests of Upper Key Largo comprise of some of the most diverse forest of the continental United States, containing over 120 tree species. The forests are a mixture of deciduous and evergreen broadleaf tree species (Tomlinson 1986, Robertson 1955). The evergreen species are mostly of West Indian origin. Canopy height is low in these forests in comparison with other tropical dry forests of the world, and average 8-12m in height (Hilsenbeck 1976, Ross et al. 1992). Basal area is high in comparison with other tropical dry forests are all 1999). These diverse forests are built upon comparatively shallow soils which typically do not exceed 20 cm in depth and are developed directly on Pleistocene limestone bedrock (Ross et al 1992).

The forests of Upper Key Largo are within the Tropical Dry Forest Life Zone according to Holdridge (1967), and is within Walter's (1985) Zonobiome II (tropical with

summer rain). Freezes are extremely rare in the Florida Keys; hurricanes and fires are a more important part of the disturbance regime (Ross et al, 1998).

I established experimental plots in three sites at Crocodile Lakes National Wildlife Refuge in Key Largo (all of which have been cleared): Whisky Bottle Lake, the Nike Missile, and Cock Fighting Arena. The Whiskey Bottle plot is located at the western edge of the Whiskey Bottle Lake. This plot was characterized by sparse vegetation up to 4m in height. It contained several small trees and seedlings, including fruiting *Metopium toxiferum*. Little grass and shrub species were present and much of the bedrock was exposed due to extreme degradation and clearing of the forest following a failed housing development. The Cock Fighting Arena site was also characterized by sparse vegetation and shrubs. Grasses and shrubs covered most of the ground with very few small trees established. There was one larger tree approximately 5m tall with wide branches stretching over 6m. The Nike Missile plot was located on a former military base. The plot established there was the site of a building that had been cleared and removed. There were several small trees and shrubs established up to 6m in height, although most remnant vegetation was not above 3m in height.

Seed Sampling.

In order to examine species richness of local fruiting vegetation, I devised eight 4m x 50m transects for each plot. There were two transects on each side of each plot. One transect occurred along the edge of the forest, and the other transect 10m within the forest. I collected seeds from any plant falling within the transects; the whole plant did not have to fall within the transects for seeds to be collected from that particular plant.

The plant of each seed collected was identified and recorded. Each transect was sampled twice between 1 May and 1 September.

Seed Dispersal

I set up experiments at three study sites within Crocodile Lakes National Wildlife Refuge (Whiskey Bottle Lake, Cock Fighting Arena, Nike Missile Site). Each site contained 1 50m² plot of disturbed forest. Each plot contained five paired seed traps (perch vs. non-perch) randomly placed throughout the plot. Each paired seed trap was 1 m² and 2 meters apart. The artificial perches were placed directly in the center of one of the paired seed traps, while the second trap in the pair was free from overhanging vegetation. Seed traps consisted of fine mesh cloth material (Illustration 1) of one square meter. Seed rain was measured in seed traps below artificially erected perches as well as from paired seed traps with no over-hanging perch. Each perch was approximately 6 m tall and 1 meter in diameter; fallen tree branches were used as artificial perches because they were found to be more effective than human-made crossbar perches (Holl, 1998; see also Illustration 1).

The traps consisted of a fine mesh cloth material. Seeds were collected from seed traps on a weekly basis. All seeds were counted and identified. The following figure illustrates this design:

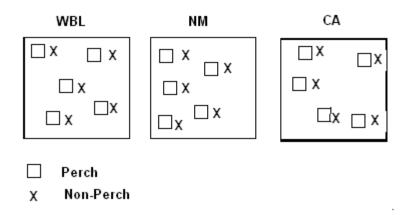


Figure 1. Experimental design of three sites. WBL = Whiskey Bottle Lake; NM = NikeMissile, and CA = Cock-fighting Arena site. Each site is approximately 50 m².

Bird Utilization of Perches.

Using binoculars, bird visits to the plots were recorded on 3 non-consecutive afternoons for two hours between 1800-2000 h at each plot without rain and heavy wind. Each plot was also observed three times in the morning between 0600-0800 h to account for variation in species recorded due to time of day. All perches were observed including artificial perches I placed in the plots, as well as small remnant trees in the plots. I recorded the species and approximate height on the perch in which each bird landed on each artificial remnant tree perch. This procedure was followed throughout the study.



Illustration 1. Artificial perch with seed trap below and paired trap to the left.



Illustration 2. Poisonwood seed collected in seed trap.

Bird Sampling

In order to examine species richness of local avifauna, I prepared eight, 4 m x 50 m transects for each plot. There were two transects on each side of each plot. One transect occurred along the edge of the forest, and the other transect was placed 10m from the edge of the forest. Transects were walked at 0600 and 1800 h and all birds seen during the transect walk were recorded. Each transect was sampled twice.



Illustration 3. White-crowned Pigeon within edge transect

RESULTS

Seed Rain

Seed rain was significantly higher within seed traps below branch perches when compared to paired traps without overhanging perches; no bird-dispersed seeds were found in seeds traps without perches. Within the four month study, 503 total seeds were collected (Table 1). Of the 503 seeds collected, 96% were of *Ficus citrifolia*. Three were *Metopium toxiferum* and two seeds from *Passiflora suberosa* were collected from the seed traps. Thirteen seeds were unidentified. Two of the three identified species were of mid-level forest species, indicating perches may aid in regrowth of mid-level and mature forests (Ross et al 2001). Of all the seeds collected, 488 individual seeds were of midlevel successional species, and 2 seeds were of early successional species.

		Seed	Number of
Common Name	Scientific Name	Туре	Seeds
Short Leaf Fig	Ficus citrifolia	М	485
	Metopium		
Poisonwood	toxiferum	М	3
Corky-stemmed	Passiflora		
Passion-flower	suberosa	E	2
Unident.			13

Table 1. Table illustrating seed types. M represents mid-level succession forest species, and E represents early

Seeds collected were dominated by mid-level successional species. I found a significant difference between the arrival of seeds from late and early successional species in traps (Chi square = 4.099, df = 1, p<.05) (Whiskey bottle site data were not used due to small sample size) (Table 2); this analysis assumes that early and late successional seeds have an equal chance of arrival in seed traps. This latter assumption may be violated, however, if one successional type is significantly more abundant in terms of seeds than the other.

	Early	Late	Total
Whiskey	0	5	6
Arena	1	44	45
Missile	1	452	453
Total	3	501	504

Table 2. Chi-Square analysis table. Whiskey site data was not used as chi square could not be calculated with a 0 variable.

	Early	Late	Total
Whiskey	0	4	4
Arena	1	4	5
Missile	1	20	21
Total	2	28	30

Table 3. Chi-Square analysis table showing number of dispersal events to seed traps in early and late successional species

These patterns were also apparent when comparing dispersal events. Seed dispersal events for late successional species far outnumbered dispersal events for early successional species (Chi-square = .05, df = 1, p = .823).

For plant seeds that arrived into seed traps, I examined whether or not nearby seed sources were present based on plant transects sampled along the forest edge and interior forest at each site. No clear patterns were apparent (Table 3a, Table 3b) when examining sites independently; in some cases, plants were found adjacent to the sites, in others not.

Edge Transects	Forest Transects	S
<u>Species</u>	Species	
short leaf fig	1citrifolia	5
Poisonwood	10wild coffee	8
fish poison tree	2poisonwood	11
wild lantana	22fish poison tree	3
	gumbo limbo	4
	Short leaf fig	1
	wild lantana	13

 Table 4. Data of all fruiting plants/trees recorded within transects across plot

	Presence of <i>Ficus citrifolia</i> in Seed Trap	Presence of <i>Ficus citrifolia</i> in Edge Transect
Whiskey	+	• .
Arena	+	-
Missile	+	+
	Presence of <i>Motopium</i> toxiferum in Seed Trap	Presence of Metopium toxiferum in Edge Transect
Whiskey	-	-
Arena	+	-
Missile	+	+
	Presence of <i>Passiflora</i> suberosa in Seed Trap	Presence of <i>Passiflora suberosa</i> in Edge Transect
Whiskey	-	-
Arena	+	-

Missile

Table 5a. Presence/absence data of seeds found in seed traps and plant transects at the forest edge.

+

	Presence of Ficus citrifolia in Seed Trap	Presence of Ficus citrifolia in 10m Forest Transect
	Seeu ITap	TUIN FOREST TRANSECT
Whiskey	+	+
Arena	+	-
Missile	+	-
	Presence of Metopium toxiferum in Seed Trap	Presence of Metopium toxiferum in 10m Forest Transect
Whiskey	<u>.</u>	+
Arena		
	+	-
Missile	+	+
	Presence of Passiflora	Presence of Passiflora suberosa
	suberosa in Seed Trap	in 10m Forest Transect
Whiskey	-	-
Arena	+	-
Missile	+	-

Table 5b. Presence/absence data of seeds found in seed traps and along plant transects within nearby forest interior (see Methods).

However, a pattern is evident when comparing the relationship of each seed species found in seed traps across all sites and edge and forest transects. To examine these results I used the Fisher Exact Test. A positive relationship was recorded for each seed species in relation to edge (Shortleaf fig P1 = .5, P2 = 1, Poisonwood, P1 = 1, P2 = 1, corkscrew P1 = 1, P2 = 1) and 10m (Shortleaf fig P1 = .5, P2 = 1, Poisonwood, P1 = 1, P2 = 1, corkscrew P1 = 1, P2 = 1) forest transects. Two of the 3 seeds identified within forest plots were also found present within edge and 10m forest transects, indicating a potential relationship between seeds dispersed beneath perches and those found in surrounding edge forests. The only species not found within the forest (corkscrew), was found growing within the plot itself.

	Presence of Ficus citrifolia in	Presence of Ficus citrifolia in
	Seed Trap	Edge Transect
All plots	+	+
-	Presence of Metopium	Presence of Metopium toxiferum
	toxiferum in Seed Trap	in Edge Transect
	+	+
	Presence of corkscrew in Seed	Presence of corkscrew Edge
	Тгар	Transect
	+	-

Table 6a. Presence/Absence data of seeds found in all traps (all 3 sites) and seeds found in all edge transects (all 3 sites).

	Presence of Ficus citrifolia in Seed Trap	Presence of Ficus citrifolia in 10m Forest Transect
All plots	+	+
	Presence of Metopium toxiferum in Seed Trap	Presence of Metopium toxiferum in 10m Forest Transect
	+	+
	Presence of corkscrew in Seed Trap	Presence of corkscrew in 10m Forest Transect
	+	-

Table 6b. Presence/Absence data of seeds found in all traps (all 3 sites) and seeds found in all 10m within forest transects (all 3 sites).

Bird Visitation

Five species of birds were observed at artificial perches, and eight species were

observed on tree perches. A total of eight species were observed on all perches. Sixty-

two percent of bird species utilizing perches were seed dispersers. However, this

difference was not significant in comparison to non-seed dispersers ($P_1 = 1.00$, $P_2 = 1.00$)

indicating perches may not be effective in attracting certain bird types (seed/non seed dispersers).

Seed Dispersing	Non-Seed Dispersing
Individuals	Individuals
26	3

Table 7. Number of bird individuals observed to use artificial perches in study sites that are known to disperse seeds and those that do not.

Fourteen total bird individuals were observed using artificial branch perches,

while 29 total individuals were observed using remnant tree perches, for a total of 43

perch visits. There was no significant difference among sites (alpha = .05, Z = 2.394)

regarding usage of branch perches among sites (P = .1239).

		Bird Type	No.
Common Name	Scientific Name	(Disperser/Non)	Visits
Northern Cardinal	Cardinalis cardinalis	Disperser	28
Prairie Warbler	Dendroica discolor	Disperser	6
White-Crowned Pigeon	Columba leucocephala	Disperser	2
Eastern Phoebe	Sayornis phoebe	Disperser	3
Short-eared owl	Asio flammeus	Non seed disperser	1
Great-Creasted flycatcher	Myiarchus crinitus Ardea (herodias)	Disperser	1
Great white heron	occidentalis	Non seed disperser	1
Turkey Vulture	Cathartes aura	Non seed disperser	1

Table 8. Number of total visits to artificial and remnant tree perches. Seed dispersers are birds that were observed or are reported to remove fruits and potentially disperse plant seeds. Some bird species may also destroy seeds during seed-handling or gut passage

Common Name	Scientific Name	Mean Height (m) R	lange
Northern Cardinal	Cardinalis cardinalis	4.08	.5-10m
Prairie Warbler	Dendroica discolor	2.83	.5-10m
White-Crowned Pigeo	n Columba leucocephala	6	6m
Eastern Phoebe	Sayornis phoebe	5	5m
Short-eared owl	Asio flammeus	5	5m

Table 9. Mean height on perch of birds visiting perches.

During bird censuses along transects, a total of 32 individual birds were recorded in forest edge transects and 16 individuals were identified in forest transects located 10 m inside forest, representing 6 and 4 species, respectively (Table 6). Eight total species were identified within both transects. The approximate height at which each bird individual landed on the artificial perches were also recorded (Table 9).

There was no significant difference between all bird species observed visiting perches versus those observed in all transects (alpha = .05, Z = 2.394, P = .957). However, there was a closer match between bird species that visited perches and those that were found in edge transects (alpha = .05, Z = 1.960, P = .5860), than birds found in 10m forest transects (alpha = .05, Z = 1.960, P = .2246).

A. Bird Transects Edge Transects		10m Transects			
Species	Total # of Individuals		Species White-crowned	Total # of Individuals	
White-crowned Pigeon		14	Pigeon	10	
Red-cockaded Woodpecker		2	Northern Cardinal	2	
Great-creasted Flycatcher		2	Brewers Black Bird	2	
Northern Cardinal		12	Indigo Bunting	2	
Turkey Vulture		1			
Great White Heron		1			
Totals		32		16	48

Table 10. Total number of birds observed in all forest edge and forest interior (10m) transects surrounding study plots.

DISCUSSION/CONCLUSION

Seed Rain

As supported in several other studies conducted in a tropical setting, seed rain was significantly increased do to perches (McDonnel & Stiles 1983; McDonnell 1986; McClanahan & Wolfe 1987, 1993, Aide and Caelier 1994; Wunderle 1997, Miriti 1997, Holl 1998, Shiels, 2003, Zanini and Ganade, 2005) In this study, seed rain was dominated by a single species, *Ficus citrifolia*, which is a relatively abundant fruiting species in Upper Key Largo, with each fruit producing a large number of seeds; *Ficus Citrifolia* occurs in mid-successional forest (Ross et al 2001). *Metopium toxiferum* was also recorded, though at much lesser densities than *Ficus citrifolia*, and is also a midsuccessional tree which inhabits forest at least 50-75 years of age (Ross et al, 2001). Seeds of these species were also the only tree species collected from seed traps, suggesting that using perches to facilitate seed dispersal may be a very local event. There are over 120 species of trees identified within these forests, yet two, representing the two species observed within the experimental transects, were collected over a 4 month period in 2006. The availability of nearby seed sources may be a significant consideration if the goal of a restoration project is to restore to previous biodiversity. Additional efforts may be needed to bring seeds of native forest species if dispersal by local bird species is indeed distance-limited.

In previous studies, most of the seeds dispersed (Aide and Cavelier 1994, Holl 1998) were from early successional, shrub seeds already present in the disturbed research area. However, in my study, most species collected were from mid-successional forests and tree species, as there were a small number of shrubs present in the disturbed plots, indicating (according to the results of previous studies) that plots with less established vegetation may increase the relative ratio of later successional species if close to intact forest and seed sources. It is apparent that seeds that are closest to the perches including early successional seed species found within the same degraded patches the perches are placed and meant to restore, will have the most effect on seed rain. These links have not been clearly established in the past, as all seed rain is not necessarily "desirable" seed rain in terms of native forest recovery. The only non-forest species (*Passiflora suberosa*) found in seed traps within this study was also one of the few fruiting shrubs found within the degraded plots.

There are many considerations involved in forest restoration and the use of perches in reestablishing forests. Perches do not overcome subsequent barriers to regeneration such as seed survival and seedling establishment. Higher seed rain does not guarantee higher seedling establishment (Miriti 1997, Holl 1998). Dispersed seeds and resulting seedlings may have to cope with intense competition from established vegetation. Studies conducted in pastures show intense competition with grasses which may severely limit the growth of certain plants (Nepstad et al. 1991, Guariguata et al. 1995, Sun & Dickinson 1996).

Bird Visitation

There is a high percentage of plants that have fleshy fruits in tropical forests relative to temperate forests (Howe & Smallwood 1982; Fleming 1991); therefore I expected to find a high rate of seed dispersers utilizing the perches than non-seed dispersers. A total of 8 species of birds were observed using both branch and trees as perches. Five of these eight species are known seed eaters. Fourteen individuals were observed on branch perches, and 29 individuals were observed using tree perches for a total of 43 recorded visits.

All birds observed utilizing perches were also observed along edge and forest interior transects. This study identified a positive relationship between bird communities of surrounding forests and those utilizing perches. There was greater relationship between bird species recorded utilizing all perches and those recorded in edge transects rather than forest interior transects, indicating edge effects may support a greater diversity of bird species and forest-edge bird species may play a chief role in the use of perches in disturbed forest.

The height of the perch in which each bird landed was also recorded as an extra measure, with the most important insights to these results being that different species tend to land on varying heights, and some species didn't seem to have a particular preference in regards to height of the perches present within each plot. Birds landed on all levels of the perches, from .5 to 10m in height. This supports the hypothesis that perch complexity may be beneficial to attract more species and individuals as different bird species fly and utilize different heights (McDonell and Stiles, 1983). Cardinals landed on a wide range of the perches and were highly active. They were recorded landing from approximately .5m to 10m of both artificial and tree perches. Prairie warblers were found low, utilizing the lower 1m to 2.5m of the perches, and were often within the upper canopy of trees surrounding the transects. White-crowned pigeons were also seen regularly flying high over and across the plots, yet were only recorded landing within the plots twice. This may explain their low occurrence within the disturbed plots; although at high abundance

within surrounding forests, they may simply prefer higher perches. The white-crowned pigeon is a major seed disperser in the area and is largely credited with the diversity of these forests, dispersing tropical seeds from the West Indies. If the effectiveness of this management practice is to be maximized, more work is required to examine ways to attract birds occupying several niches and flight zones, and even targeting keystone dispersers such as the white-crowned pigeon.

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