Role of frugivorous birds in promoting succession in montane forests of the Talamanca Mountain Range: A case study in Piedra Alta, Costa Rica

Juston W. Jaco

ABSTRACT

In the deforested highland montane regions of Costa Rica, restoration ecologists have recognized the potential of frugivorous birds as seed dispersers in forest regeneration. My objective is to understand which frugivorous bird species spend their time perched in forested and non-forested habitats, and to note on which plant species they perch, and their respective sizes. I seek to answer two primary questions: (1) is it possible to reforest disturbed habitats utilizing patterns of avian seed dispersion? and (2) what are alternatives to current land management techniques (e.g. which vegetation could be planted in disturbed habitats to attract multiple bird species)?

To answer these two questions, I conducted research from 2–22 April 2013 in the Talamanca Mountain Range of Costa Rica (along the top headwaters of Río Buena Vista–Rio General Watershed in Cordillera de Talamanca) in the village of Piedra Alta, between 9°30'–9°32'N and 83°34'–83°48'W, at an elevation of approximately 2200 m. Transects that bordered each other were chosen to observe which bird species were utilizing both natural forests and disturbed habitats. Three transects were located within natural forests, two within disturbed habitats, and one along a road in a disturbed habitat. In the case of Piedra Alta, I identified 11 frugivorous bird species in both forested and non-forested habitats that could act as candidates for seed dispersal. However, based on the literature of Stiles and Skutch (1989), other candidates for seed dispersal were recognized, although they were not seen in the unaltered forested zones. Limitations of this study stem from the local farmers of Piedra Alta, the instructors at ICADS and myself in our collective abilities to identify plant and bird species, which makes our observational capacity somewhat less than if identification were performed by professional botanists or ornithologists.

RESUMEN

En los bosques montañosos deforestados de Costa Rica, los ecólogos de restauración han reconocido el potencial de las aves frugívoras como dispersores de semillas para la regeneración del bosque. Mi objetivo es comprender cuales especies de aves se perchan en ambos hábitats forestales y no forestales, y notar cuales especies de plantas se posan las aves y su tamaño relativas. Quiero responder a las siguientes preguntas: (1) ¿es posible reforestar los bosques alterados utilizando los patrones de la dispersión de semillas por los aves? y (2) ¿hay alternativas posibles a la gestión actual de la tierra? (p. ej. ¿qué tipo de vegetación debe permanecer o debe plantarse en los hábitats perturbados para atraer múltiples especies de aves?)

Para contestar estas preguntas, hicé la investigación entre el 2 y el 22 de abril del 2013 en la Cordillera de Talamanca de Costa Rica (a lo largo de las cabeceras superiores del Río Buena Vista y el Río Cuenca general en la Cordillera de Talamanca) en la localidad de Piedra Alta, entre los 9°30'–9°32'N and 83°34'–83°48'O, a aproximadamente 2200 m elevación. Los transectos que bordeaban uno al otro fueron elegidos para observar cuáles especies de aves estaban utilizando tanto los bosques naturales como los hábitats perturbados. Hubo tres transectos que se encontraban dentro de los bosques naturales, dos en áreas con hábitats perturbados, y un a lo largo de una carretera en el interior de un hábitat similarmente alterado. En el caso de Piedra Alta, identifiqué 11 especies de pájaros frugívoros tanto en los hábitats forestales como no forestales que pueden funcionar como candidatos a la dispersión de semillas. Sin embargo, debido a la literatura de Stiles y Skutch (1989), otros candidatos para la dispersión de las semillas fueron reconocidos, aunque no se observaron en el bosque natural. Algunos sesgos fueron de mis propias limitaciones, las de los agricultores locales de Piedra Alta y las de los instructores de ICADS en nuestra capacidad de identificar las plantas y las aves, que hacen que nuestras observaciones sean menos acertadas que si se basaran en las de ornitólogos o botánicos profesionales, respectivamente.

INTRODUCTION

The Talamanca Mountain Range, found between 2100 and 3300 meters, extending from southeastern Costa Rica to western Panama, presents a unique location for conservation biology studies. Here, birds are considered catalysts in extending natural montane forests into disturbed and altered forests. A seed disperser that eats berries and seed-containing fruits can transport seeds to new areas through droppings, potentially extending forest vegetation. Bird presence can ultimately generate multifaceted, dense woodland preserves via their role in seed dispersal. Consequently, this study focuses on avian species of the highland forests of Costa Rica that fly frequently from forest fragments to adjacent pastures and degraded habitats. Seed dispersers found in both disturbed and non-disturbed habitats are potential candidates for forest regeneration in altered habitats distant from parent trees—a process known to increase biodiversity during succession (Hooper *et al*. 2005; Gomes *et al*. 2008). Succession in cleared habitats and abandoned pastures is dependent upon forest seeds that arrive to these areas (Holl 1999). Here I consider seed dispersal patterns in currently active sites, in contrast to previous studies that have analyzed forest regeneration through seed dispersers in abandoned pastures (Kappelle 1993; Aide *et al*. 1995; Nepstad *et al*. 1996; Holl 1998; Duncan and Chapman 1999; Holl 1999; Zimmerman *et al*. 2000; Hooper *et al*. 2002; Hooper *et al*. 2004; Hooper *et al*. 2005).

In the Talamanca Mountain Range, habitat restoration has favored selective planting of indigenous hardwoods to restore gradually abandoned agricultural plantations and cattle pasturelands (Greig & Webster 1992; Norman 1998). However, systematically planting trees in order to return the forest to its original condition is expensive and not an economically viable option to accelerate the regrowth of a disturbed forest (Norman 1998). Any restoration that has occurred at the farm level is most often limited to the planting of exotic species or native alders (Kappelle & Juárez 1995). Though allowing natural succession to regenerate disturbed habitats is an option to reforestation, this becomes problematic because rates of regrowth in montane forests take much longer when soils are heavily impacted (Chazdon 2003) and when temperatures remain cooler throughout the year (Kappelle 1993); as a result, landowners have highly unproductive plots with little to no economic value in highly disturbed regions (E. Araya *pers. comm.*). Forest restoration and management practices are needed that concurrently accelerate natural regeneration and promote economically and socially valuable forest products (Parrotta *et al*. 1997). Today, it is in Costa Rica's interest to replace degraded montane highlands with forest cover, since agricultural production is decreasing each year (E. Araya *pers. comm.*).

Nonetheless, intact pristine montane forests remain standing, which may aid in local recovery processes and spur economic growth. Remnants act as corridors between disturbed zones as well as a means of movement for seed-dispersing birds (Slocum and Horvitz 2000; Barrantes and Pereira 2002; Chazdon 2003). Remnant woodlands promote forest extension—species richness, tree density and aboveground biomass (Guariguata and Ostertag 2001). In the Talamanca Mountain Range, birds are a vital component in the maturation of disturbed habitats, and are an economically viable solution to accelerate forest growth (Norman 1998). At high-elevation montane forests, where fewer plant species depend on wind or water currents for dispersal (and where bats, which may also act as dispersers, are less numerous), birds play an even greater role in seed dispersion (Forsyth & Miyata 1984). This has implications for conservation and restoration strategies in areas that have decreased total biomass throughout its former geographic range. Identifying which frugivorous birds spend time in both forested and non-forested zones will allow conservationists the opportunity to understand the kinds of vegetation (recruitment foci) these species perch on; from here, land managers can plant specific vegetation preferences of the frugivorous birds in the non-forested zones so that they can easily travel beyond the intact natural forested zones. Thus, birds as seed dispersers can not only regrow foliage into previous ranges, but also develop overall structure into a more complex, layered woodland preserve with sustainable economic potential.

Prior to this study only six frugivorous bird species were recognized as candidates for seed dispersal into non-forested montane regions, but I hypothesized that there are more than six candidates for the acceleration of growth in this region, due to the limited and fixed hours of sampling sessions during the study and the literature of Stiles and Skutch (1989) of known frugivorous highland bird species. I also expected to sample until the species accumulation curve leveled off within both the forested and the non-forested areas. Since the species accumulation curve did not level off after two days of observation, I varied observation hours of transects to ensure that I would see the greatest number of bird species, as the circadian rhythm of individual species varies.

METHODS

Study area

I sampled from 2–22 April 2013 in the Talamanca Mountain Range, along the top headwaters of Río Buena Vista–Rio General Watershed in Cordillera de Talamanca. Study areas were located in the village of Piedra Alta, between 9°30'–9°32'N and 83°34'–83°48'W at approximately 2,200 m elev. The climate of Piedra Alta, like most other areas of the highlands, is moderately wet (rainfall averages between 2,000–3,000 mm) and has a dry season from December to April (Oostra *et al*. 2008). Adjacent to Piedra Alta is Villa Mills, with an average annual temperature of 10.9°C (Instituto Meteorológico Nacional 1988). Water is abundant in these montane forests: around half (80 to 100 inches) is in the form of rainfall while the other half becomes available through horizontal precipitation, where water particles from clouds condense against vegetation, which gives this region the name "cloud forest" (Norman 2012). In comparison to other tropical rainforests, temperatures vary significantly, fluctuating from 25°C during the day to below freezing at night (Norman 2012). Throughout the montane forest understory, tree seedlings, palms and large patches of bamboo are supported by high moisture levels from horizontal precipitation, especially in the afternoons during the wet season from May to November (Kappelle 1993; Norman 2012).

This region is home to tall forests (approximately 45 – 50 meters) with dense, high branches and fairly compact crowns; these contain more biomass of wood per acre than any other forest in Costa Rica (Norman 2012), though secondary forests are easily distinguishable from primary forests. Primary (mature old-growth and species-rich) and secondary (recovering, much shorter with lower basal area) *Quercus* forests dominate the tropical montane evergreen forests of Piedra Alta (Kappelle 1993; Sillett 1994; Helmer *et al*. 2000). This region has experienced significant habitat conversion and environmental alteration in a relatively short amount of time. At the turn of the twentieth century, Costa Rica's increasing human population triggered an expansion up the country's mountain slopes, and by 1943, the Inter-American Highway was finally completed, increasing freight travel to and from Panama (Helmer *et al*. 2000; Oostra *et al*. 2008).

From the 1950s to the 1970s, the upper montane oak forest was further cleared due to the demand for commercial logging, agricultural plantations and cattle pastures, and colonization (Kappelle 1993; Helmer *et al*. 2000; Oostra *et al*. 2008; Norman 2012). These demands contributed to an extremely heterogeneous arrangement of vegetation on lands that were inappropriate for such practices in the first place, due in part to the local climate, soil conditions and steepness of the land (Helmer *et al*. 2000; Barrantes and Pereira 2002). Sites left untouched can be credited to Costa Rica's abrupt topography, which appears to have stalled the destruction of the montane forest (Barrantes and Pereira 2002). By the 1980s, the Chirripo National Park, Los Santos Forest Reserve and Rio Macho Forest Reserve were created to protect the remaining natural forests of Costa Rica. These and other protected locations prohibited landowners, farmers and charcoal producers from cutting or burning forest without authorization (Kappelle & Juárez 1995; Oostra et al. 2008; Norman 2012). This was essential for the preservation of montane habitats and for restoring some level of environmental quality.

However, extensive protective zones were economically devastating for many who depended on the income from the logging and charcoal production. Those who did not leave began raising cattle and cultivating monocultures of blackberries on whatever land they had (Helmer *et al*. 2000), furthering land degradation, while others created lodging cabins and offered guided tours. Yet this has yet to see much monetary success (Norman 2012). The switch from charcoal to agricultural production and cattle pastures has not preserved the land any better than previous logging techniques.

Data Acquisition in Transects and Habitats

Preliminary data collection for this research project began on 8 March 2013 in Villa Mills with instructors David Norman, Kat Peters and Gabriel Vargas, and a group of seven students including myself from the Institute for Central American Development Studies (ICADS). During two consecutive mornings (6 am to 8:30 am), we walked slowly and quietly through two different birding sites; each individual had binoculars for observation. We were also equipped with copies of *A Guide to the Birds of Costa Rica* by Stiles and Skutch (1989) to place observed birds into taxonomic categories. Additionally, substrate type, perch type and perch size were recorded. The experience gained during this exercise was critical for data collection in Piedra Alta.

The transects of this site were moderately to severely sloped, interspersed with a matrix of isolated trees, shrubs, blackberry crops and patches of remnant montane forests spared during deforestation. The introduction of dairy cattle in the early 1990s gave way to the planting of grasses *calinguero* (no scientific name found) and *Pennisetum clandestinum*, which is native to East Africa (E. Araya, *pers*. *comm*.). At the time of this study, cattle pastures had not been removed from the land and cattle were being raised in combination with blackberry monocultures (Figure 1). The owners of land on which I made my observations on mentioned that they did not allow cutting trees or charcoal making on their property (E. Araya, *pers*. *comm*.). Recent logging was not evident at any sites I studied.

I laid out six transects in forested and non-forested areas to assess bird and plant perch species. There were three transects located within intact primary forests (approximately 135m, 150m and 195m in length), two transects located within disturbed areas with scattered trees (*Cupressus lusitanica* and *Quercus costaricensis*) and cattle pastureland within a matrix of extensively used agricultural land for blackberries (approximately 135m and 265m in length). One transect was located along a road within a disturbed habitat that was between cattle pastures and blackberry patches (approximately 475m in length). I totaled the number of steps for each transect four times, walking two times in each direction to get an average, as almost all transects ended up containing steep slopes. I used a measuring tape to obtain the average number of steps it took me to walk ten meters; I then converted the average of my paces of each transect to meters.

I selected transects that bordered or were adjacent to each other to see which bird species were using both natural forest and non-forested zones. In this study, natural forests were defined as all stretches of continuous forest that had been left untouched by humans; non-forest was defined as stretches of road, cattle pastures and/or blackberry patches within a mosaic of remnant forest vegetation. To avoid damage to sloping terrain, all transects followed the contours of the landscape and previously made footpaths, especially within the three transects of the natural forest.

Using these six transects, I spent two-thirds of the sampling sessions in non-forested habitat and one-third of the time in the natural forest habitat. More time was spent within the non-forest habitats to observe which frugivorous species were actively utilizing the disturbed habitat—these birds are critical to forest restoration. All observations took place in the morning from 6:30 to 9:30 am under fair weather (light winds and clear to partly cloudy skies), except the last 4 days of observations when rain and wind made birding observations difficult. Additional sampling sessions were made on three Sundays (2 to 5 pm) with two afternoons spent along transects of the non-forest and one along transects of the natural forest). All afternoon sampling sessions were under cloud-covered skies and heavy fog. In total, 14 sampling sessions were made in the non-forested habitats and 7 in the natural forest habitats for a total of 21 days (63 hrs.) of observations. I also frequently changed the order and direction of each transect I walked so that I was not always at the exact same place at the exact time each morning.

Method of Bird and Plant Identification

I was equipped with a pair of binoculars (Nikon Egret 8 x 40) and a list of bird and plant species most commonly found within the Talamanca Mountain high-elevation region. Compared to the number of bird and plant species in the Caribbean lowlands, Costa Rica's montane forests have less than a third the number of bird species and a high dominance of oak trees—two species of oak trees represent over 60% of total plant biomass (Norman 2012). Thus, the range of bird and plant species found at higher elevations is notably smaller than the range of species at lower elevations. Stiles and Skutch (1989) was used for avian identification while plant identification came from the complied research of Kappelle (1996), León and Poveda (1999), and Alfaro-Vindas (2003).

Unknown bird and plant species presented limitations. While I had thorough descriptions and sharp photographic images of unknown species, not all birds or plants could be identified. Moreover, I recognize my limitations as well as those of the ICADS instructors and the local farmers of Piedra Alta in our collective abilities to identify bird and plant species, which makes our observations less reliable than if they were based on a professional ornithologist or botanist. By the end of the study, unidentifiable birds were excluded, but unidentifiable perch sites used by frugivorous birds were kept. Identified birds observed outside the survey time or that were flying above transects were also excluded. Additionally, some were observed several times flying over both forest and non-forest transects, like the American Swallow-tailed Kite (*Elanoides forficatus*). This species is known to eat fruits, and thus could potentially aid in reforestation efforts (Stiles and Skutch 1989), but since it was never seen perched in either the natural forest or non-forested zones, it was also excluded from this study. Finally, birds perched or foraging were identified on a daily basis to obtain a species accumulation curve. Also known as the species discovery curve, this graph recorded the cumulative number of avian species found as a function of the cumulative hours spent searching for them.

Methods of Bird and Plant Sampling

Bird and plant species were recorded opportunistically as I walked through each study site; the majority of avian species were recorded visually, but a few were recorded aurally with the help of local residents for confirmation. When I was unable to identify a species, I took detailed notes on its color, tail, mandible, posture, movement and behavior (if possible), labeling the unknown bird morpho-species 001, 002, etc. until it could be placed into an appropriate taxonomic category. The same is true of plant perches; any species that I was unable to identify was, again, described in detail and photographed with a Nikon (Coolpix AW100), and then the leaves were cut, pressed and labeled accordingly, to have them identified either by local farmers or an ICADS instructor. Pressed leaves were stored in the refrigerator (4.5°C) and were labeled unknown plant morpho-species 001, 002, etc.

Tree Height Measurements

After I cut a fallen branch to the length of my arm, I would hold my arm out straight with the cut branch pointing vertically so that it forms a 90° angle to my outstretched arm. Using the flattest path I could (in relation to the tree I was measuring), I walked backwards until the tip of the branch lined up with the top of the tree. At this point, my location was roughly the same distance from the tree as it was high. I then counted my steps to the tree and converted them to meters using the same method as for transect lengths. For trees on elevated patches of land or off transects, I estimated the height by comparing the heights of nearby trees. To classify vegetation height, categories were made for short (height < 10.5 m), medium ($10.5 <$ height < 25.5 m) and tall (height ≥ 25.0 m).

RESULTS

I identified a total of 38 bird species throughout the duration of this study. There were eight species found only in the forest, 11 species found only in the non-forest and 19 species found in both the forest and the non-forest (Table 1). Of the 19 species found in both forested and non-forested habitats, 11 were frugivorous: *Catharus gracilirostris* (Black-billed Nightingale-Thrush), *Piranga bidentata* (Flame-colored Tanager), *Parula gutturalis* (Flame-throated Warbler), *Pezopetes capitalis* (Large-footed Finch), *Ptilogonys caudatus* (Long-tailed Silky-flycatcher), *Turdus plebejus* (Mountain Robin), *Chlorospingus pileatus* (Sooty-capped Bush-Tanager), *Catharus ustulatus* (Swainson's Thrush), *Tiaris olivacea* (Yellow-faced Grassquit), *Pselliophorus tibialis* (Yellow-thighed Finch), and *Vireo carmioli* (Yellow-winged Vireo) (Tables 1 and 2).

Except for the Black-billed Nightingale-Thrush and Large-footed Finch, all other observed frugivorous species were seen perched on *Cupressus lusitanica* (Table 2). The Black-billed Nightingale-Thrush and Large-footed Finch were only observed foraging on fallen logs, in leaf litter and under large vegetation like *Cupressus lusitanica*. As a result, perching sites are not available for these two species (Table 2). The remaining nine frugivorous birds (except the Mountain Robin and Yellow-winged Vireo) perched on *Quercus costaricensis*, but this observation may be due to the fact that there were fewer total observations of them, leading to a smaller sample size when compared to that of the Rufous-collared Sparrow (*Zonotrichia capensis*) and Collared Redstart (*Myioborus torquatus*) (Tables 1 and 2). These results indicate the importance of avian species' behaviors (e.g. flight from dense forest into open disturbed habitat) and perching/habitat preferences (e.g. high up in treetops vs. leaf litter), as influences on whether or not seeds will be deposited in the non-forest.

Other important perching sites included *Rubus laciniatus*, which was used by six species (Flame-colored Tanager, Mountain Robin, Sooty-capped Bush-Tanager, Yellow-faced Grassquit, Yellow-thighed Finch, Yellow-winged Vireo) and *Quercus copeyensis*, which was visited by 5 species (Flame-colored Tanager, Flame-throated Warbler, Large-footed Finch, Long-tailed Silky Flycatcher and Mountain Robin) (Table 2). The fact that many observations were made on *Rubus laciniatus* can be accredited to the pasture my transect went through, as it encompassed an extensive blackberry cultivation site.

With respect to smaller shrubs like those of *Rubus laciniatus*, the Sooty-capped Bush-Tanager and Yellow-thighed finch were frequently seen foraging in brushy openings and lower undergrowth like *Rubus eriocarpus*, *Bomarea hirsuta*, *Tithonia diversifolia* and *Palicourea sp.*; those were the only species observed on these plant species in non-forested zones. The Yellow-faced Grassquit and Yellow-thighed Finch also often visited *Chusquea sp*. while the Sooty-capped Bush-Tanager and Yellow-faced Grassquit both perched on the smaller *Miconia sp*. (Table 2). The Flame-colored Tanager and Swainson's Thrush utilized a species locally known as *titora* (no scientific name found).

Some perching sites were only used by certain species. The Swainson's Thrush was spotted on *Podocarpus macrostachyus*, *Myrica pubescens* and *Vaccinium sp*.; the Flame-colored Tanager was occasionally seen on a grueso (no scientific name found) and *Brugmansia sp*.; the Flame-throated Warbler was a common visitor *Quercus seemannii*; and the Sooty-capped Bush-Tanager was observed perched on *Macleania rupestris*. These were intermittent and rarer compared to *Cupressus lusitanica*, *Quercus copeyensis* and *Quercus costaricensis*, which dominated the transect sites (Table 2).

Results from perching sites also indicate the importance of non-vegetation structures and dead standing trees as sites for seed dispersal, as seen by Barrantes and Pereira (2002). Of the nine species that frequent perching sites (except the Sooty-capped Bush-Tanager and Yellow-thighed Finch who visited shrubbery), they perched on a variety of dead standing vegetation including *Cupressus lusitanica*, *Quercus copeyensis* and *Quercus costaricensis* of all sizes as well as on fence posts and waterlines (Table 2), possibly watching for predators. There were no differences among bird perching heights (Figure 2), although Duncan and Chapman (1999) and Slocum and Horvitz (2000) found that the amount of seeds dispersed by perched frugivorous birds at the tree's base depended on tree height; accordingly, taller trees received more perched frugivorous birds and seed droppings than smaller trees.

Holl (1998) suggested that even though non-vegetation structures tend to increase seed dispersal, they typically do not overcome barriers to establishment, such as seed predation and low seed germination due to land degradation. For this reason, non-vegetation structures will not be considered in the discussion, but remnant dead standing vegetation will be, since Holl (1998) found that bird visitation rates were significantly higher on branches than on artificial crossbar perches and, consequently, had a higher number of dispersed seeds below branch perches than crossbar perches.

The species accumulation curve (Figure 3) indicates that the total number of species observed is most likely not representative of the total number of avian species in the forest and non-forested zones because both curves are increasing (neither curve plateaus to provide an estimate of avian richness). With increased effort expended sampling, both curves would be expected to decelerate. According to Stiles and Skutch (1989), there are 61 known avian species that are found with the highland regions of Latin America, and in combination with migratory and other commonly found birds that are not considered endemic, the total of avian species increases to just over 100 in the Talamanca Mountain Range. In this study, I observed 56 species (38 of which were identifiable), which is about half of their observations. However, its important to note that these numbers were estimated over two decades before this study was conducted, and their findings of avian density, species type, and habitat preference, may not necessarily be appropriate for extrapolating data today.

DISCUSSION

After 14 sampling sessions totaling 63 hours, 11 avian species (Black-billed Nightingale-Thrush, Flame-colored Tanager, Flame-throated Warbler, Large-footed Finch, Long-tailed Silky-flycatcher, Mountain Robin, Sooty-capped Bush-Tanager, Swainson's Thrush, Yellow-faced Grassquit, Yellow-thighed Finch and Yellow-winged Vireo) entered into the pool of important candidates for forest restoration in Piedra Alta. They are known to eat varied seeds and to fly from pristine forest fragments to adjacent pastures and degraded habitats far from parent trees.

These species and their habitat preferences shed light on alternative ways montane forests can be brought back from their degraded condition throughout Costa Rica. Of these 11 species, the Black-billed Nightingale-Thrush and Large-footed Finch were not seen on any perching sites, suggesting that they may not be ideal candidates for forest regeneration because they do not utilize remnant vegetation or other structures away from the forest's edge. This is not to say that these two species cannot disperse seeds into non-forested habitats, but land managers cannot plant preferred vegetation if it is nonexistent.

Thus, the trees that these nine remaining frugivorous species use as perches are key indicators for land managers, as they act as important recruitment foci for seed dispersers in disturbed habitats (Slocum and Horvitz 2000). All frequented varying sizes of *Cupressus lusitanica* and 7 species (Flame-colored Tanager, Flame-throated Warbler, Long-tailed Silky-flycatcher, Sooty-capped Bush-Tanager, Swainson's Thrush, Yellow-faced Grassquit, Yellow-thighed Finch) were perched on medium and large *Quercus costaricensis* (Table 2). An additional important perching site included *Quercus copeyensis*, which was visited by 5 species (Flame-colored Tanager, Flame-throated Warbler, Large-footed Finch, Long-tailed Silky Flycatcher and Mountain Robin) (Table 2). While *Cupressus lusitanica* was the most common perching site due to its relative abundance, this species does not fruit and will not be considered important for seed dispersers' diet. Hence, *Quercus costaricensis* and *Quercus copeyensis* are the 2 most important plant species for attracting the largest number of frugivorous birds and should be planted within the matrix of cattle pastures and blackberry patches of Piedra Alta.

However, there are other factors, such as bird habitat preference, that must be considered if land managers want to increase bird visitation on recruitment foci. Planting just *Quercus costaricensis* and *Quercus copeyensis* is not expected to accelerate growth of disturbed habitats when other frugivores do not perch on them. While sampling, it became clear that different vegetation attracts particular avian species (Slocum and Horvitz 2000). For smaller perching sites such as low shrubbery, *Rubus eriocarpus*, *Bomarea hirsuta*, *Tithonia diversifolia* and *Palicourea sp*. could be valuable planting options for the Sooty-capped Bush-Tanager and Yellow-thighed Finch, as they were frequently seen foraging in brushy openings and lower undergrowth vegetation structures (Table 2). *Chusquea sp*. was a perching site for the Yellow-faced Grassquit and Yellow-thighed Finch while *Miconia sp*. was for the Sooty-capped Bush-Tanager and Yellow-faced Grassquit (Table 2).

Zimmerman *et al*. (2000) found that the number of seeds under remnant vegetation decrease with distance from adjacent forests. Therefore, planting a mix of the aforementioned species in the disturbed habitats away from natural forests may increase the rate of secondary succession. Some plant species would potentially have to be planted in later successional stages (depending on the conditions of the land), as strong barriers to establishment would prohibit their growth relative to adjacent forested zones (Nepstad *et al*. 1996; Zimmerman *et al*. 2000). Nonetheless, the compiled results in Table 2 indicate that enhancing the biodiversity of vegetation (and their respective sizes) in non-forested zones can only increase the amount of perching observations one would see, thereby increasing the probability of varying seed dispersal.

At the same time, one must consider avian species that were observed far less frequently in only one habitat and those that were not detected in either habitat (again, this is due to the extensive bird observation data from Stiles and Skutch). For example, the duration of this study does not account for migratory frugivorous birds, each with their own movement patterns, preferred plants, and perching sites, which illustrates the need for multi-season and multi-year data collection (Loiselle & Blake 1991). My observations, in combination with the literature from Stiles and Skutch (1989), indicate that *Columba fasciata* (Band-tailed Pigeon), *Columba* *subvinacea* (Ruddy Pigeon), *Catharus frantzii* (Ruddy-capped Nightingale-Thrush) and *Turdus nigrescens* (Sooty Robin) may have more of an important role in the reforestation of highland montane forests than some previously mentioned frugivorous species, such as the Yellow-faced Grassquit, Flame-colored Tanager, Black-billed Nightingale-Thrush and Large-footed Finch. Observations of the Yellow-faced Grassquit were 3 times more abundant in the non-forested areas than in natural forest (Table 1), and the species is known to strictly visit weedy fields, pastures, roadsides and lawns with seeding grasses (Stiles and Skutch 1989). Because the Yellow-faced Grassquit frequents these areas more often and disperses seeds already in these pastures, one would expect seeds from the forested zones to be consumed at a lower rate. The same is true for the Flame-colored Tanager, which was observed nine times more within non-forested habitat than natural forest (Table 1). This is surprising because the Flame-colored Tanager's preferred habitat is mountain forest treetops, although it is known to venture into pasture (Stiles and Skutch 1989). Here may be a limitation of experimental decision (that dense foliage limited treetop visibility), or an observation that its preferred habitat has shifted to mainly non-forested zones. In the case of the Black-billed Nightingale-Thrush, no perching was observed on trees (Table 2), similar to the Large-footed Finch, who was also only seen on the ground. Consequently, the Yellow-faced Grassquit, Flame-colored Tanager, Black-billed Nightingale-Thrush and Large-footed Finch may not be ideal candidates for reforestation even if they are frugivorous.

These observations are due to each bird's preferred habitat and foraging behavior. Thus, the goal of selective planting is to utilize what we know of their behavior and habitat preference to plant vegetation that will allow them to venture further into disturbed habitats to disperse seeds. Planting species used by frugivorous birds (Table 2) near the borders of the forested zone (and at increasing intervals into non-forested zones) may increase frugivorous presence within non-forested zones, principally catalyzing natural regeneration similar to the nucleation model of forest recovery of Yarranton & Morrison (1974). Guevara and Laborde (1993) and Carrière *et al*. (2002) found that trees facilitated woody seedling establishment in non-forested zones, but Aide *et al*. (1995) found that low-lying shrubs also are key; in both findings, the result is an increased likelihood of dispersal under remnant vegetation in comparison to open grassland, also indicated by Duncan and Chapman (1999). The difference is that the types of vegetation seem to attract distinct frugivorous birds who then disperse distinct seeds.

The significance of frugivores' behavior is that intermediate disturbed habitats (a hybrid of forest and non-forested zones or the natural forests' outermost edges) are sites for regeneration (Hooper *et al*. 2004). For example, larger frugivores avoided open areas with severe habitant disturbance whereas smaller frugivores entered open areas with greater tolerance (Gomes *et al*. 2008). Large species such as the Band-tailed Pigeon and Ruddy Pigeon, on the other hand, are known to frequent mountainous country that is at least partly forested and to perch high in tree canopies; the Band-tailed Pigeon takes *Myrica* and Rapanea fruit and *Phytolacca* berries while the Ruddy Pigeon takes mistletoe berries and assorted fruit (Stiles and Skutch 1989). In fact, the Ruddy Pigeon has a diet of only fruit, and since this species was observed only in non-forested areas (and not in its preferred habitat of forest canopy or secondary forest), it is a good indication that this species can act as a candidate for seed dispersal (Table 1). Planting fruiting *Myrica*, Rapanea and *Phytolacca* as well as mistletoe berries will likely increase Band-tailed Pigeon and Ruddy Pigeon presence in natural forest, mobilizing dispersal of seeds to adjacent pastures. This indicates that Gomes *et al*. (2008) cannot overgeneralize bird behavior strictly on their size because, as indicated by the Band-tailed Pigeon and Ruddy Pigeon, larger species indeed enter severely disturbed habitats and were only seen in non-forested zones in this study.

The Sooty Robin consumes a variety of fruits and berries of Ericaceae, *Solanum*, and melastomes that makes it an excellent disperser in cordilleras (Stiles and Skutch 1989). This provides an opportunity for land managers to selectively plant Ericaceae, *Solanum*, and melastomes within the mosaic of extensive blackberry patches already in place. These same species can be planted in open expanses of disturbed páramo, open bogs, and low second growth since the Sooty Robin forages in these locations (Stiles and Skutch 1989). The Ruddy-capped Nightingale Thrush also avoids perching sites in treetops but instead lurks in wet mountain forest undergrowth and neighboring bamboo and secondary growth thickets in relatively open areas (Stiles and Skutch 1989). Because this species was found only in non-forested zones and not its preferred habitat (Table 1), this is a sign that it may be a candidate for seed dispersal. When the Ruddy-capped Nightingale Thrush did venture out into forest, it was only seen at clearings near natural forest. This species, although less commonly observed (Table 1), also visits pasture, but only pasture with adjoining vegetation (Stiles and Skutch 1989), indicating that planting bamboo and tall secondary growth (e.g. structures mimicking thicket habitats) along and within the disturbed habitat will be important if this species is to disperse seeds outside of the natural forest. The Ruddy-capped Nightingale-Thrush stands in sharp contrast to the Buffy-crowned Wood-Partridge (*Dendrortyx leucophrys*) and Buffy-fronted Quail-Dove (*Geotrygon costaricensis*); while they do consume many fruits and seeds, they almost always lurk within the understory of montane forests, seldom venturing out into clearings to disperse fallen seeds (Stiles and Skutch 1989). The Buffy-fronted Quail-Dove also visits secondary growth and the ground around thickets, but is not known to leave woodland areas (Stiles and Skutch 1989). Thus, the Buffy-crowned Quail-Dove and Buffy-fronted Quail-Dove are not candidates for forest regrowth (Table 1).

CONCLUSION

The problem is no longer disappearing forests in the Talamanca Mountain Range, but diminishing land quality. However, it may be possible to restore disturbed habitats utilizing patterns of avian seed dispersion. From information gathered from local families, it was clear they knew how degraded their land was (they currently have to buy fertilizer for their blackberry crop, which was unnecessary a decade ago) and what measures should be taken to improve its quality. They understood the importance of birds as seed dispersers, the benefits of having large oaks hold soil in place on steep slopes, and the challenges they will face without the regeneration of the forest or the recovery of degraded soils. Farmers of Piedra Alta, with their extensive patches of cattle pastureland and blackberry monocultures, need sustainable land management alternatives that will benefit its current degraded condition, as well as the native and migratory birds that utilize the land, before it is abandoned. Given the fact that farmers today know the state of degradation their land is in and that many cannot afford to take away from cattle pastures or blackberry crops to selectively reforest disturbed habitats, new polices and governmental incentives are needed to continue preservation in the twenty-first century. For the avian candidates and their preferred perches found in this study to be used to their fullest potential, there needs to be collaboration between governing bodies, restoration ecologists, and local farmers.

Although several national wilderness reserves were created in the 1980s by Costa Rica's government, new alternatives of conservation are needed throughout montane forest ecosystems today, especially if seeds dispersed by birds are to germinate in active pastures. For example, I found that medium and large *Quercus costaricensis* and *Quercus copeyensis* were the 2 most important plant species for attracting the largest number of frugivorous birds, so they should be planted in addition to the smaller *Rubus eriocarpus*, *Bomarea hirsuta*, *Tithonia diversifolia*, *Palicourea sp*., *Chusquea sp*., and *Miconia sp*. to increase plant heterogeneity. My results suggest that enhancing the biodiversity of vegetation in non-forested zones would increase the amount of bird perching observations, thereby increasing the probability of seed dispersal. The method of *selective* planting is an alternative dependent on bird behavior and habitat preference, or better said, is the key in allowing birds to venture further into disturbed habitats to disperse seeds, thereby accelerating forest regeneration. The combination of these plant species may facilitate woody seedling establishment in non-forested zones better than in open grassland.

I suggest that Costa Rica's government offers monetary incentives for restoration efforts, as landowners are more likely to upkeep and preserve the land if they benefit economically by doing so (Leigh 2002). My host family tended their blackberry plots and cattle pastures every day from 6 am to 4 pm; thus, finding time to work with organizations to reforest, for example, would be a difficult time commitment to make, at least during the dry season when blackberry production is active. Blackberry production usually ends in March and starts again in late August or early September. When blackberry plots are no longer fruiting, many landowners of Piedra Alta will sell some of their cattle to make a living. The government and/or NGOs need to participate actively within the community to get members involved and educated on reforestation techniques as well as have them compensated for their time and effort. Consistent land maintenance and care that permit property owners to benefit economically from their land improvements is indispensable to sustainable land development (Leigh 2002). What landowners will gain from this interaction has a fundamental value in both understanding how to work with nature and how to respect natural processes.

Further research

While *Rubus laciniatus* (blackberry) was the most common small perching site in the non-forested habitat for six species (Flame-colored Tanager, Mountain Robin, Sooty-capped Bush-Tanager, Yellow-faced Grassquit, Yellow-thighed Finch, Yellow-winged Vireo), it should be eliminated from the kinds of vegetation critical to reforestation because the non-forest habitat is already covered with this species. Planting more blackberry patches will not necessarily aid in forest regeneration, which is why the focus of further studies in Piedra Alta should focus on seed rain of forest and successional forest species away from blackberry patches. Seeds of species already in the pasture are not critical in this respect. Additional studies should verify if there are differences among bird perching heights, as one was not observed in this study (Figure 2). However, the Sooty-capped Bush Tanager and the Yellow-thighed Finch were more inclined to visit small perches (ten and seven sites, respectively), whereas the Long-tailed Silky Flycatcher and Swainson's Thrush avoided small perching sites and visited medium to large perches (five and nine sites, respectively) (Table 2). Again, understanding the ecological behavior of each frugivorous bird will be critical for the selection of plant vegetation structures. Random planting will not necessarily better natural forest restoration efforts, particularly if plants do not produce seeds for a frugivores' diet (e.g. *Cupressus lusitanica*).

It would be interesting to study how widely seeds are dispersed from nearby forests into pasturelands and to assess if seeds of woody species can establish themselves there. The extent that microclimatic conditions and soil physical and chemical parameters affect seedling germination will also be informative as demanding environmental conditions (e.g. heavy soil compaction) seem to affect seed germination (Aide and Cavelier 1994; Guariguata and Ostertag 2001; Chazdon 2003), though the relative importance of these barriers to establishment varies greatly with soil type, existing vegetation, climate and management history (Holl 1999; Zimmerman *et al*. 2000). For example, many areas within the pastures of Piedra Alta have observable exposed roots and loose soil (Figure 4); the question of whether dispersed seeds can even germinate becomes critical to assess, especially when stresses are worsened by invading exotic grasses that compete with tree seedlings (Hooper *et al*. 2002). Blackberry production and cattle farming have been ongoing for the past three decades, further eroding soil horizons in Piedra Alta. This means that recovery of soil fertility may be a prerequisite before deposited seeds can even germinate (Holl 1999).

Forest seedling availability (and avian seed dispersal) into non-forested regions is the limiting factor for forest regeneration (Nepstad *et al*. 1996), and even when seeds arrive to these regions, tropical montane vegetation regeneration is limited at all early stages of succession: colonization, establishment, growth and survival (Holl 1999; Hooper *et al*. 2004). Holl (1999) proposes that planting native woody seedlings to increase canopy structure, setting up bird perching structures and planting bushy vegetation that matures and fruits quickly may be viable options to overcome barriers to seed dispersal. However, even if these barriers are overcome, many interacting factors may effect seed germination, growth and survival, which is why it will be mandatory to pinpoint rate-limiting factors at individual sites to create the best site-specific management plan tailored to the needs of the disturbed habitat for forest regeneration to occur (Holl 1999).

ACKNOWLEDGMENTS

I am tremendously appreciative of and grateful to the Araya-Mena family of Piedra Alta with whom I stayed during the month of my independent research project. I am thankful for Edwin Araya for his patience and his field assistance as he helped me locate transects to walk in the natural forest. Edwin, Aracelly and Ricardo, were ready to lend a hand anytime I needed assistance in the identification of vegetation. The people of Piedra Alta were considerate when answering my questions about previous land use and I appreciate that they allowed me to study on their land. To the very supportive ICADS instructors David Norman, Gabriel Vargas and Kat Peters, I am grateful they aided me in preliminary bird watching sessions in Villa Mills, and encouraged me to return to the Talamanca Mountain Range to develop this project; our line of communication was always open and I felt at ease knowing I could contact them with any questions or concerns. They truly provided valuable insight into the role of frugivorous birds in promoting succession in montane forests. This paper benefited from the reviews and comments by J. Foufopoulos, B. Low, S. Malamis, D. Norman, K. Peters, and B. Siniakov. The fieldwork for this research was supported by the University of Michigan, to which I am obliged.

Figure 1: Extensively-grazed pastureland with patches of *Rubus laciniatus* and forest fragments of old growth and second-growth in the Talamanca Mountain Range of Costa Rica.

Figure 2. Heights of perching sites (vegetation and non-vegetation) from Piedra Alta, Provincia San José, Costa Rica April 2–22, 2013. Perch heights are based on the following increments: Short = height < 10.5 m, Medium = 10.5 < height < 25.5 m) and Tall = height ≥ 25.0 m.

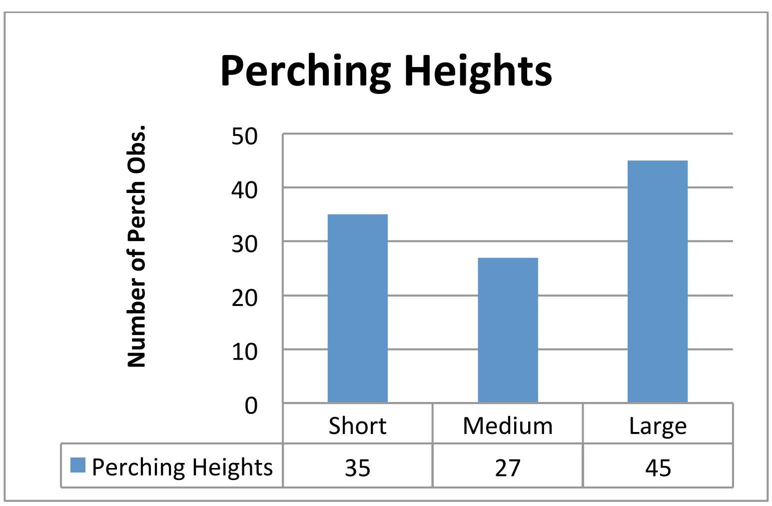

Figure 3. Species Accumulation Curve (Species Discovery Curve) from Piedra Alta, Provincia San José, Costa Rica April 2–22, 2013. Graph records the cumulative number of avian species found in forest vs. the non-forest as a function of the cumulative number of sampling sessions (hours) spent searching for them.

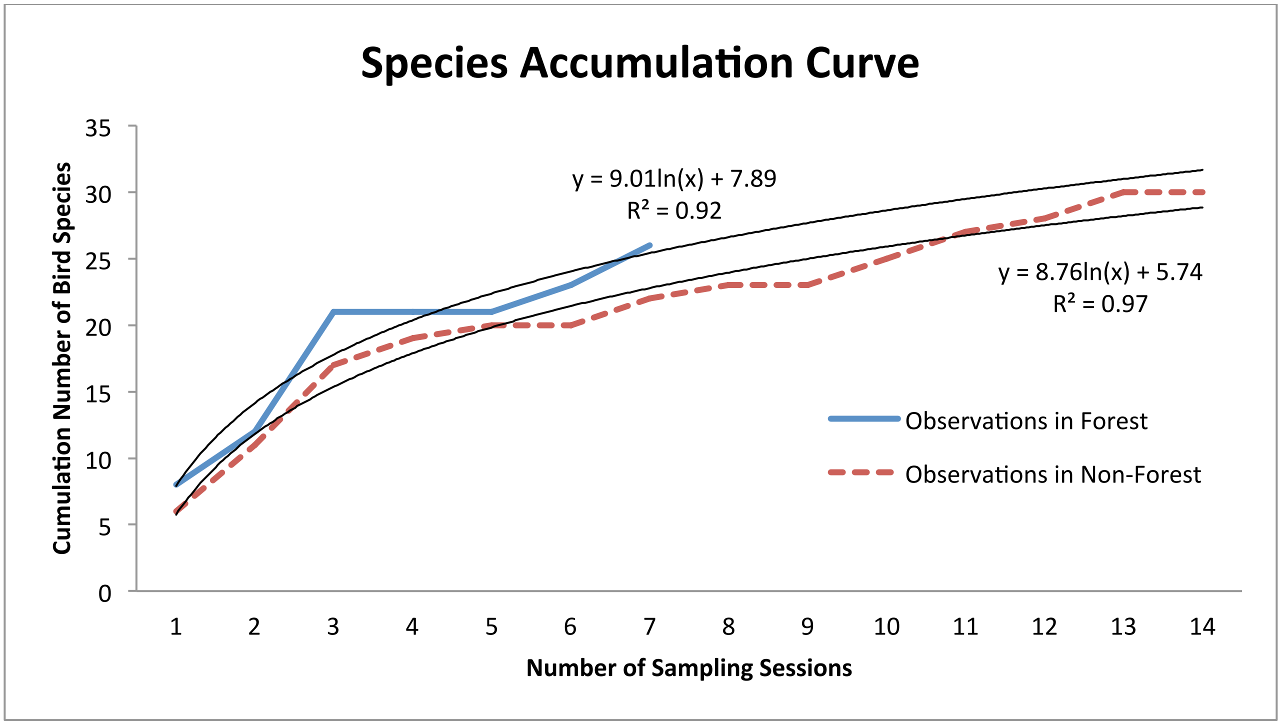

Figure 4: Exposed root structures and soil horizons layers were common throughout transects in the non-forested zones.

Table 1. Birds observed in Piedra Alta, Provincia San José, Costa Rica April 2–22, 2013. Dietary and habitat information are placed in order of importance according to Stiles and Skutch (1989). Diet: C = carnivore; F = frugivore; G = granivore; I = insectivore; N = nectarivore. Habitat: A = agricultural plantations; F = forests; P = pastures (in general, brushy clearings, fields and adjacent clearings with scattered, remnant forest trees, open country páramo and garden and dooryard shrubbery); R = ravines; S = second growth; U = urban areas.

Common Name (*Scientific Name*)	Diet	Habitat	No. Obs. In Forest	No. Obs. in Non-Forest	Candidate for Reforestation
Acorn Woodpecker (*Melanerpes formicivorus*)*	G, I	F, P	2	9	No
Band-tailed Pigeon (*Columba fasciata*)	G, F	F	0	7	No (But likely)
Black Vulture (*Coragyps atratus*)	C, F	T, P, F	0	2	No
Black-billed Nightingale-Thrush (*Catharus gracilirostris*)*	I, F	F, S, P	6	12	Yes (Not likely)
Black-capped Flycatcher (*Empidonax atriceps*)	I	F, S, P	0	8	No
Black-cheeked Warbler (*Basileuterus rufifrons*)	I, F	R, F, P	18	0	No
Blue-and-white Swallow (*Notiochelidon cyanoleuca*)	I	U, A, F	0	5	No
Buffy-crowned Wood-Partridge (*Dendrortyx leucophrys*)	G, F, I	F, S	2	0	No
Buffy-fronted Quail-Dove (*Geotrygon costaricensis*)	F, G, I	F	2	0	No
Collared Redstart (*Myioborus torquatus*)*	I	F, R, P, S	24	15	No
Fiery-throated Hummingbird (*Panterpe insignis*)	N	F, S	5	0	No
Flame-colored Tanager (*Piranga bidentata*)*	I, F	F, P, A	2	18	Yes (Not likely)
Flame-throated Warbler (*Parula gutturalis*)*	I, F	F, P, R	6	9	Yes
Gray-breasted Wood-Wren (*Henicorhina leucophrys*)	I	F, R, S	3	0	No
Gray-tailed Mountain Gem [*Lampornis* (*castaneoventris*) *cinereicauda*]	N	F, S	1	0	No
Hairy Woodpecker (*Picoides villosus*)*	I	F, S, P	2	2	No
House Wren (*Troglodytes aedon*)	I	S, P, F, A	0	2	No
Large-footed Finch (*Pezopetes capitalis*)*	G, I, F	R, F, S, P	15	8	Yes
Long-tailed Silky-flycatcher (*Ptilogonys caudatus*)*	I, F,	F, S	2	9	Yes
Mountain Robin (*Turdus plebejus*)*	G, F, I	F, P, S	2	15	Yes
Ruddy Pigeon (*Columba subvinacea*)	F	F, S	0	3	No (But likely)
Ruddy Treerunner (*Margarornis rubiginosus*)*	I	F, P	1	1	No
Ruddy-capped Nightingale-Thrush (*Catharus frantzii*)	I, F	F, R, S, P	0	2	No (But likely)
Rufous-collared Sparrow (*Zonotrichia capensis*)*	G, I	U, P, A, S	3	146	No
Scintillant Hummingbird (*Selasphorus scintilla*)	N	F, P, S, A	2	0	No
Sooty Robin (*Turdus nigrescens*)	I, F, G	P, S, F	0	5	No (But likely)
Sooty-capped Bush-Tanager (*Chlorospingus pileatus*)*	I, F	F, S, P	10	15	Yes
Spotted-crowned Woodcreeper (*Lepidocolaptes affinis*)*	I	F, P, S	3	3	No
Swainson's Thrush (*Catharus ustulatus*)*	F, G, I	F, S, U, P	7	16	Yes
Townsend's Warbler (*Dendroica townsendi*)	I	F, S, P	0	2	No
Volcano Hummingbird (*Selasphorus flammula*)*	N	P, S, F	1	9	No
Western Wood-Pewee (*Contopus sordidulus*)	I	F, P	0	3	No
Wilson's Warbler (*Wilsonia pusilla*)*	I	F, S, A, P	1	4	No
Yellow-billed Cacique (*Amblycercus holosericeus*)	I, F	S, F, R	1	0	No
Yellow-faced Grassquit (*Tiaris olivacea*)*	G, F, I	P	6	22	Yes (Not likely)
Yellow-thighed Finch (*Pselliophorus tibialis*)*	I, F, N	F, S, R, P	14	11	Yes
Yellow-throated Bush-Finch (*Atlapetes gutturalis*)	I, G, F	S, F, A, P	0	1	No
Yellow-winged Vireo (*Vireo carmioli*)*	I, F	F, P, S	4	4	Yes

Table 2. Frequently visited perching sites of the 11 frugivorous birds that forage both in the forest and non-forested regions of Piedra Alta, Provincia San José, Costa Rica April 2–22, 2013. Vegetation sizes are based on the following categories: Short = height < 10.5 m; Medium = 10.5 < height < 25.5 m; Tall = height ≥ 25.5 m.

Common Name ***Scientific Name***	**Characteristic Perching Sites and Sizes of the Non-Forest**		
Black-billed Nightingale-Thrush *Catharus gracilirostris*	N/A		
Flame-colored Tanager *Piranga bidentata*	Short Perches *Rubus laciniatus* *Fence post	Medium Perches *Brugmansia sp.* Cleyera theaeoides Grueso (no scientific name) *Dead standing tree *Waterline	Tall Perches *Cupressus lusitanica* *Quercus copeyensis* *Quercus costaricensis* *Morpho-plant species 017 *Dead standing tree
Flame-throated Warbler *Parula gutturalis*	Short Perches *Dead standing tree	Medium Perches *Quercus Seemannii*	Tall Perches *Cupressus lusitanica* *Quercus copeyensis* *Quercus costaricensis*
Large-footed Finch *Pezopetes capitalis*	N/A		
Long-tailed Silky-flycatcher *Ptilogonys caudatus*	Short Perches	Medium Perches *Quercus copeyensis* *Quercus costaricensis* *Dead standing tree	Tall Perches *Cupressus lusitanica* *Quercus costaricensis*
Mountain Robin *Turdus plebejus*	Short Perches *Rubus laciniatus* *Fencepost *Unidentifiable shrubs	Medium Perches *Cupressus lusitanica* *Quercus copeyensis*	Tall Perches *Cupressus lusitanica*
Sooty-capped Bush-Tanager *Chlorospingus pileatus*	Short Perches *Bomarea hirsute* *Macleania rupestris* *Miconia sp.* *Palicourea sp.* *Rubus eriocarpus* *Rubus laciniatus* *Tithonia diversifolia* *Morpho-plant species 010 *Morpho-plant species 012 *Morpho-plant species 016	Medium Perches *Quercus costaricensis* *Morpho-plant species 011	Tall Perches *Cupressus lusitanica*

Common Name *Scientific Name*	**Characteristic Perching Sites and Sizes of the Non-Forest**		
Swainson's Thrush *Catharus ustulatus*	Short Perches	Medium Perches *Cleyera theaeoides* *Cupressus lusitanica* *Myrica pubescens* *Podocarpus macrostachyus* *Vaccinium sp.* *Dead standing tree	Tall Perches *Cupressus lusitanica* *Quercus costaricensis* *Morpho-plant species 007
Yellow-faced Grassquit *Tiaris olivacea*	Short Perches *Miconia sp.* *Rubus laciniatus* *Fencepost *Unidentifiable shrubs	Medium Perches *Chusquea sp.* *Dead standing tree	Tall Perches *Cupressus lusitanica* *Quercus costaricensis* *Dead standing tree
Yellow-thighed Finch *Pselliophorus tibialis*	Short Perches *Bomarea hirsute* *Cupressus lusitanica* *Rubus eriocarpus* *Rubus laciniatus* *Tithonia diversifolia* *Palicourea sp.* *Unidentifiable shrubs	Medium Perches *Chusquea sp.* *Quercus costaricensis* *Morpho-plant species 011	Tall Perches *Quercus costaricensis*
Yellow-winged Vireo *Vireo carmioli*	Short Perches *Rubus laciniatus* *Fencepost	Medium Perches	Tall Perches *Cupressus lusitanica*

*Indicates unidentifiable dead standing plant species or non-vegetation structures.

REFERENCES

Aide, T. M. and Cavelier, J. (1994): Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta. *Restoration Ecology*, **2**: 219-229.

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

Alfaro-Vindas, E. (2003): *Plantas Comunes del Parque Nacional Chirripó*, Costa Rica. Santo Domingo, Heredia, Costa Rica: Instituto Nacional de Biodiversidad.

Barrantes, G. and Pereira, A. (2002): Seed dissemination by frugivorous birds from forest fragments to adjacent pastures on the western slope of Volcán Barva, Costa Rica. *Revista de Biología Tropical*, **50**. Electronic Copy.

Carrière, S. M., Andre, M., Letourny, P., Olivier, I., and McKey, D. B. (2002): Seed rain beneath remnant trees in slash-and-burn agricultural system in southern Cameroon. *Journal of Tropical Ecology*, **18**: 353-374.

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

Duncan, R. S. and Chapman, C. A. (1999): Seed dispersal and potential forest succession in abandoned agriculture in tropical Africa. *Ecological Applications*, **9**: 998-1008.

Forsyth, A. and Miyata, K. (1984): Chapter 7 - Eat Me. *Tropical Nature*, Charles Scribner's Sons, New York.

Gomes, L. G. L., Oostra, V., Nijman, V., Cleef, A. M., and Kappelle, M. (2008): Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biological Conservation*, **141**: 860-871.

Greig, N. and Webster, M. (1992): The role of remnant trees in forest regrowth in cattle pasture. *Organization for Tropical Studies*, **92**:3. Print.

Guariguata, M. R. and Ostertag, R. (2001): Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, **148**: 185-206.

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

Helmer, E. H., Brown, S., and Cohen, W. B. (2000): Mapping montane tropical forest successional stage and land use with multi-date Landsat imagery. *International Journal of Remote Sensing*, **21**: 2163-2183.

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

Hooper, E. R., Legendre, P., and Condit, R. (2002): Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. *Ecological Applications*, **12**: 1626-1641.

Hooper, E. R., Legendre, P., and Condit, R. (2004): Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology*, **85**: 3313-3326.

Hooper, E. R, Legendre, P., and Condit, R. (2005): Barriers to forest regeneration of deforested and abandoned land in Panama. *Journal of Applied Ecology*, **42**: 1165-1174.

Instituto Meteorológico Nacional de Costa Rica. (1988): Catastro de las series de precipitaciones medidas en Costa Rica. Ministerio de Recursos Naturales, Energía y Minas. San José. 363 p.

Kappelle, M. (1993): Recovery following clearing of an upper montane Quercus forest in Costa Rica. *Revista de Biología Tropical*, **41**: 47-56.

Kappelle, M. and Juárez, M. E. (1995): Agro-ecological zonation along an altitudinal gradient in the montane belt of the Los Santos Forest Reserve in Costa Rica. *Mountain Research and Development*, **15**: 19-37.

Kappelle, M. (1996): Los Bosques de Roble (Quercus) de la Cordillera de Talamanca, Costa Rica: Biodiversidad, Ecologia, Conservacion y Desarrollo. Heredia, Costa Rica: Instituto Nacional de Biodiversidad.

Leigh, E. (2002): A magic web: the forest of Barro Colorado Island. Oxford University Press: Oxford. Print.

León, J. and Poveda, L. (1999): Los Nombres Comunes de las Plantas en Costa Rica. San José, Costa Rica: Editorial Guayacan.

Loiselle, B. A., and Blake, J. G. (1991): Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology, **72**: 180-193

Nepstad, D. C., Christopher, U., Pereira, C. A., and Cardoso da Silva, J. M. (1996): A comparative study of tree establishment in abandoned pasture and mature forest of Eastern Amazonia. *Oikos*, **76**: 25-39.

Norman, D. (1998): Role of frugivorous birds in promoting succession in montane forests of the Talamanca Range. ICADS. San José, Costa Rica. Photocopy.

Norman, D. (2012): Montane forest ecosystem in Costa Rica: some information. Institute for Central American Development Studies Courseback: Curridabat, Costa Rica.

Sillett, T. S. (1994): Foraging ecology of epiphyte-searching insectivorous birds in Costa Rica. *The Condor*, **96**: 863-877.

Slocum, M. G. and Horvitz, C. C. (2000): Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology*, **149**: 51-62.

Stiles, G. and Skutch, A. (1989): A Guide to the Birds of Costa Rica. Cornell University Press: Ithaca, New York.

Oostra, V., Gomes, L. G. L., and Nijman, V. (2008): Implications of deforestation for the abundance of restricted-range bird species in a Costa Rica could-forest. *Bird Conservation International*, **18**: 11-19.

Parrotta, J. A., Turnbull, J. W., and Jones, N. (1997): Catalyzing native forest regeneration in degraded tropical lands. *Forest Ecology and Management*, **73**: 271-277.

Yarranton, G. A. and Morrison, R. G. (1974): Spatial dynamics of a primary succession: nucleation. *Journal of Ecology*, **62**: 417-428.

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