# Bird Perches Increase Forest Seeds on Puerto Rican Landslides

Aaron B. Shiels[1,2,3] and Lawrence R. Walker[1]

## Abstract

**Landslides result in the loss of vertical vegetative structure, soil nutrients, and the soil seed bank. These losses impede timely recovery of tropical forest communities. In this study we added bird perches to six Puerto Rican landslides with three types of surfaces (bare, climbing fern, grass) in an effort to facilitate inputs of forest seeds through bird dispersal and to accelerate plant succession. Numbers of bird-dispersed forest seeds were significantly higher in plots beneath introduced perches than in control plots. Perches did not increase forest seedling densities compared with control plots. Seven different species of birds were observed on introduced perches. Because 99% of the seed inputs to controls and perch plots in the six landslides were wind-dispersed seeds (mostly graminoids), perches can improve landslide restoration if woody plants establish and shade out the dominant graminoid and climbing fern ground cover. Although increasing seed inputs from forest species is a critical step in accelerating revegetation of landslides, we suggest that supplemental restoration techniques be applied in addition to bird perches to promote forest recovery.**

**Key words: bird perches, disturbance, landslides, Puerto Rico, revegetation, seeds, seedlings, seed dispersal.**

## Introduction

Landslides are among the most severe natural disturbances in tropical rainforests (Garwood et al. 1979; Walker et al. 1996; Restrepo & Vitousek 2001) and are relatively common in Puerto Rico as a result of high rainfall events (e.g., hurricanes, tropical storms) and steep slopes (Larsen & Simon 1993). Although landslides are part of the natural disturbance regime in Puerto Rico, approximately half of the total landslides are associated with roads (Larsen & Torres Sanchez 1998), suggesting anthropogenic disturbance increases landsliding. The loss of existing vegetation and topsoil after a landslide results in the loss of vertical vegetative structure (Walker 1994), most soil nutrients (Walker et al. 1996), and the soil seed bank (Guariguata 1990). These losses make it more difficult to alleviate soil erosion and to restore rainforest communities.

The availability of plant propagules has been proposed as one of the major limiting factors for plant colonization on landslides in Puerto Rico (Walker et al. 1996). Because few seeds remain in the soil after a landslide (Guariguata 1990), plant succession depends primarily on seed rain (Restrepo & Vitousek 2001). Past studies of seed dispersal to disturbed sites in the tropics have focused on treefall gaps (Augspurger & Franson 1988; Denslow & Gomez Diaz 1990) and land clearings (Young et al. 1987; Willson & Crome 1989; Holl 1998) and only occasionally on landslides (Walker & Neris 1993). Wind is often the most common dispersal mechanism for seeds in disturbed areas, as shown in forest gaps in Panama (Augspurger & Franson 1988) and pastures in a dry forest in Costa Rica (Janzen 1988). However, the wind-dispersed species such as grasses and ferns that initially colonize tropical landslides (e.g., in Hawaii [Restrepo & Vitousek 2001] and in Puerto Rico [Walker & Boneta 1995]) may slow succession by being physically and numerically dominant for decades (Walker 1994; Wunderle 1997). Vertebrates, and especially birds, disperse seeds of mid- to late-successional trees and shrubs, particularly in wet tropical forests (Devoe 1989; Wunderle 1997). Additionally, some bird species in the tropics display preference to gaps compared with the forest understory (Schemske & Brokaw 1981; Levey 1988), though perch availability may limit seed dispersal by birds to open sites (Campbell et al. 1990). The introduction of perches may facilitate dispersal of forest seeds by birds, which may in turn accelerate plant succession on landslides. However, seed germination and seedling establishment on landslides may be further restricted by other factors, such as the availability of soil nutrients on recently eroded landslides (Shiels 2002).

Although several studies have inferred that the presence of forest seeds and seedlings below established shrubs and isolated trees was a result of seed deposition by birds (Guevara et al. 1986; Toh et al. 1999; Slocum 2001), experimental studies using introduced perches as recruitment foci are less common. Bird perches have been constructed to increase seed rain in temperate pastures (McDonnell & Stiles 1983; McDonnell 1986), temperate mined sites (McClanahan & Wolfe 1993), and tropical pastures in Costa Rica (Holl 1998) and Colombia (Aide & Cavelier 1994) but not, to our knowledge, on landslides.

In this study perches were added to landslides in Puerto

[1] Department of Biological Sciences University of Nevada, Las Vegas, 4505 Maryland Pkwy., Las Vegas, NV 89154-4004, U.S.A.
[2] Address correspondence to A. B. Shiels, email shiels@sunites.upr.clu.edu
[3] Current address: Institute for Tropical Ecosystem Studies, University of Puerto Rico, P.O. Box 23341-3341, San Juan, PR 00931-3341, U.S.A.

Rico to determine the ecological role of birds in plant succession on landslides and to test the practicality of perches to increase forest seed inputs and accelerate forest recovery on landslides. Specifically, we addressed the following questions:

(1) Does introducing perches to Puerto Rican landslides increase forest seeds and seedlings?
(2) To what extent does the local bird community use the introduced perches?
(3) Does existing vegetation ground cover (or lack thereof) affect bird visitation to perches, forest seed inputs, and forest seedling establishment?
(4) What are the restoration implications of adding bird perches to Puerto Rican landslides?

## Methods

### Study Site

This study took place on landslides between 450 and 650 m a.s.l. in the Luquillo Experimental Forest (LEF). The LEF covers roughly 110 $km^2$ (11,000 ha) in northeastern Puerto Rico, between 18°15′N–18°23′N and 65°52′W–65°48′W. Mean annual precipitation ranges from 3,000 to 4,000 mm with high year-to-year variation and little seasonality. Mean monthly temperatures range from 21 to 25°C (Brown et al. 1983; Soil Survey Staff 1995).

The natural vegetation where this study occurred is subtropical lower montane wet and rain forest *sensu* Holdridge (Ewel & Whitmore 1973). Common landslide-colonizing vegetation includes several types of grasses (e.g., *Andropogon*, *Paspalum*), thicket-forming climbing ferns (*Dicranopteris*, *Gleichenia*), other ferns (e.g., *Cyathea*, *Nephrolepis*), herbs (e.g., *Nepsera*, *Sauvagesia*), and woody colonizers, such as *Cecropia* and *Tabebuia* (Walker & Boneta 1995; Walker et al. 1996). Botanical nomenclature follows Little et al. (1974) for trees, Taylor (1994) for other flowering plants, and Proctor (1989) for ferns.

Approximately half of the 246 bird species that occur on the island of Puerto Rico are breeding permanent residents and half are nonbreeding migrants and visitors (Raffaele 1989). The LEF is home to 66 species of land birds (Wiley & Bauer 1985). Several species are found more frequently in forest gaps than in the mature forest (Wunderle et al. 1987). Over the elevational range covered by the chosen landslides, avian species diversity was similar (J. Wunderle 2001, U.S. Forest Service, personal communication).

Landslides less than 20 m wide or long were excluded from this study. From all remaining landslides in the LEF that were readily accessible (i.e., <200 m from a road), we randomly chose six landslides comprised of two landslides from each of the following three dominant ground cover types: Gleicheniaceae climbing fern (ES9, ES17), grass (ES15, ES16), and bare (>80% exposed soil; RB12, MY7). Landslides were defined by watersheds (ES, Río Espíritu Santo; RB, Río Blanco; MY, Río Mameyes; and numbered as in previous studies at these sites, e.g., see Walker & Neris 1993; Myster & Walker 1997). Dominant vegetation surrounding each landslide was noted, and elevation, area of the landslide, aspect, slope, and light intensity were also recorded for each landslide (Table 1).

### Perch Additions

On each landslide we established four circular plots (each 2 m diameter; 3.14 $m^2$) no closer than 5 m from the nearest forest edge to the center of the plot, such that each plot was at least 4 m on center from each adjacent plot as one of four corners of a square or along a straight line following the forest edge, depending on the landslide dimensions. Two of the four plots on each landslide were randomly assigned introduced perches (hereafter referred to as perches) and two plots served as controls. Perches were made from tree saplings retrieved near each landslide; stripped of leaves, flowers, and fruits; and erected to a height of 4–4.5 m above the ground. Perches were held in place by burying approximately 0.7 m of the lower section of the perch in the ground and stabilizing the perch by attaching guidewires to stakes. All perches were thinned to have approximately equal branching area (17–18 branches > 1 cm diameter at the main stem). Among the six landslides a total of three tall naturally occurring stems were trimmed to 1.3 m height to avoid complications with this study. Introduced perches were used in this study instead

**Table 1.** Site characteristics for the six landslides used for perch additions in the Luquillo Experimental Forest in northeastern Puerto Rico.

| *Site* | *Dominant Vegetation* | *Elevation (m a.s.l)* | *Area ($m^2$)* | *Aspect* | *Slope (degree)* | *Light above Canopy ($\mu$ Einsteins•$m^{-2}$•$s^{-1}$)* | *Light at Ground Level ($\mu$ Einsteins•$m^{-2}$•$s^{-1}$)* |
|---|---|---|---|---|---|---|---|
| RB12 | None; bare soil | 650 | 506 | E | 34 | 2,000 | 2,000 |
| MY7 | None; bare soil | 630 | 1,120 | NE | 25 | 2,700 | 1,370 |
| ES9 | Climbing fern | 470 | 1,444 | NW | 20 | 2,300 | 20 |
| ES17 | Climbing fern | 440 | 851 | NW | 23 | 1,975 | 60 |
| ES15 | Grass | 480 | 1,722 | NW | 30 | 2,300 | 300 |
| ES16 | Grass | 480 | 1,295 | N | 18 | 2,200 | 175 |

The area for each site was determined from a rectangle using the widest dimensions. Light intensity was determined by averaging three measurements taken between noon and 2 p.m. local time on a clear day (<10% cloud cover) at two different heights: 1 m above the ground (which was above ground cover, if present) and at ground level.

of naturally occurring perches to control for variation in living stems (e.g., stem height, foliar and fruiting density, spatial location in the landslide) and because natural perches are generally absent in most young landslides (especially bare landslides). Natural perches might therefore influence bird activity and microclimate differently than introduced perches.

#### Seeds

Within each perch and each control plot, ten 33 × 23.5-cm subplots (each 0.0776 $m^2$) were haphazardly located at least 10 cm from each other. Subplots were randomly assigned to either trap seeds or record established forest seedlings (described below). Five seed baskets were placed on the ground surface in each plot, secured with a 30-cm stake, lined with nylon cloth (3 threads/mm) to trap seeds, and finally covered with 1.3-cm metal screening to exclude rodents. Only 5% of all seeds in our study area were more than 1.3 cm in diameter and were thereby excluded from our study. Seed traps were visited every 3 weeks between 14 June 2000 and 17 August 2001. Pieces of nylon cloth were exchanged upon seed collection with clean cloths of equal size. Once seeds were collected they were identified to species using matching seed samples collected from the surrounding forest and landslides. Only diaspores at least 2 mm long were counted and identified, and each seed was categorized as bird dispersed or wind dispersed based on seed size, morphology, and reference to Devoe (1989). Wind-dispersed seeds included not only those dispersed strictly by wind but also those dispersed by gravity and one species dispersed by epizoochory (*Desmodium*). Because of the large quantity of seeds less than 1 mm in *Miconia* (Melastomaceae) fruits, the fruits collected from species in this family were counted as a single bird-dispersed seed if found more than 50% intact.

#### Seedlings

Each of the five seedling subplots, matching dimensions of the seed baskets, was visited in July 2000, August 2000, January 2001, June 2001, and August 2001. During each visitation the number of seedlings of bird-dispersed seeds were counted within each subplot. All bird-dispersed seeds and seedlings of bird-dispersed seeds in this study represent forest species. There were no attempts to exclude rodents from seedling establishment subplots, and subplots were not weeded at any point during the experiment. Because of the presence of existing vegetation within subplots at the beginning of the experiment, July 2000 (≤45 days after perch addition) was the period used to compare forest seedling establishment between perch and control plots with the August 2001 period.

#### Bird Observations

We conducted bird observations from 1 June 2001 to 15 August 2001 in the LEF on the six landslides that were used for perch additions. Bird observations took place from either 5:30 to 8:00 a.m. or 12:00 to 2:00 p.m. The morning observation period was used as the main sampling period because it represented the time period of most bird activity in this forest (J. Wunderle 2000, U.S. Forest Service, personal communication; A. Shiels 2001, personal observation). However, less frequent mid-day sampling was conducted at these sites to account for potential species and/or visitation differences from morning to afternoon. Avian identification was based on Raffaele (1989).

Two randomly chosen landslides were visited during each sampling day. The total time of observation at each landslide was 1 hr for the morning sampling and 0.5 hr for the afternoon sampling. All bird observations were conducted by the senior author while stationary, partially concealed by surrounding vegetation, at a distance of 5–8 m from the nearest introduced perch such that both perches were visible. Weather conditions at the time of each observation were noted. For each bird observation the bird species, the location at which birds were observed, and the total visitation time within the respective habitat were recorded. The four location categories included: on the perch, in the landslide on a natural perch, on vegetation at the forest edge (i.e., ≤15 m into the forest), or flying over the landslide without perching in landslides or at the forest edge. The observer was careful not to count the same bird twice. However, the amount of time birds spent in the landslide area was the primary focus of these observations rather than the number of individuals.

Although seasonality was not accounted for in this bird observation study, the single 3-month period of bird observation is likely to be representative, or an underestimate, of mean daily bird visitation given that all the birds observed were classified as nonmigratory (Raffaele 1989). Additionally, a past mist-capture study suggests that the resident bird populations for this area do not change seasonally except when a hurricane during the previous year disrupts bird activities (Waide 1991).

#### Statistical Analyses

The average of bird-dispersed seed totals caught at the end of the experiment below perches and controls at each landslide was compared using a Wilcoxon rank scores test ($n$ = 6 for perch and control). The average of bird-dispersed seed totals below perches was then compared among the three landslides cover classes (bare, climbing fern, grass) using a Kruskal-Wallis test. The total number of wind-dispersed seeds at each of the four plots within a landslide was first averaged to compare landslide cover classes using a Kruskal-Wallis test. However, it should be noted that sample sizes for each of the cover classes were small ($n$ = 2 for each). The number of seedlings of bird-dispersed seeds (defined by Devoe 1989) below perches and controls were compared between the July 2000 and August 2001 sampling periods using a Wilcoxon rank scores test ($n$ = 6 for each perch and each control). Frequency of bird visitation

**Table 2.** Species of seeds collected, in perches and control plots combined, on all six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico.

| | *Family* | *Life Form* | *RB12* | *MY7* | *ES9* | *ES17* | *ES15* | *ES16* | *Percent* |
|---|---|---|---|---|---|---|---|---|---|
| Bird-dispersed seeds | | | | | | | | | |
| *Alchornea latifolia* | Euphorbiaceae | Tree | | X | | | | X | 5.4 |
| *Clusia clusioides* | Clusiaceae | Tree | | | X | X | | | 1.3 |
| *Clusia rosea* | Clusiaceae | Tree | | X | X | | | X | 9.4 |
| *Guarea guidonia* | Meliaceae | Tree | | | X | | X | X | 5.4 |
| *Matayba domingensis* | Sapindaceae | Tree | | | | X | X | X | 6.3 |
| *Miconia racemosa* | Melastomaceae | Shrub | X | X | X | X | | X | 6.8 |
| *Myrsine coriacea* | Myrsinaceae | Tree | | | X | | | X | 3.1 |
| *Nectandra turbacensis* | Lauraceae | Tree | | | | | X | X | 2.3 |
| *Palicourea* spp. | Rubiaceae | Shrub | | | | | X | X | 3.1 |
| *Passiflora sexflora* | Passifloraceae | Vine | | | | X | | | 2.7 |
| *Phytolacca rivinoides* | Phytolaccaceae | Herb | | X | | | | | 0.5 |
| *Psychotria berteriana* | Rubiaceae | Shrub | | X | X | | X | | 5.9 |
| *Rourea surinamensis* | Connaraceae | Vine | | | | | X | | 0.5 |
| *Roystonea borinquena* | Araecaceae | Palm | | | | | | X | 1.3 |
| *Schefflera morototoni* | Araliaceae | Tree | X | | | X | X | X | 40.1 |
| *Schlegelia brachyantha* | Scrophulariaceae | Vine | | | | | | | 5.9 |
| Wind-dispersed seeds | | | | | | | | | |
| *Andropogon bicornis* | Poaceae | Graminoid | X | X | X | X | X | X | 27.7 |
| *Guzmania* spp. | Bromeliaceae | Bromeliad | | | X | X | | | |
| *Desmodium* spp. | Fabaceae | Herb | X | X | | X | X | | 0.9 |
| *Elephantopus mollis* | Asteraceae | Herb | X | X | | | X | | 0.9 |
| *Homalium racemosum* | Flacourtiaceae | Tree | | | | | | X | <0.1 |
| *Lasiacis divaricata* | Poaceae | Graminoid | | | | X | X | X | 0.3 |
| *Mikania* spp. | Asteraceae | Vine | | | X | X | X | X | 0.7 |
| *Paspalum conjugatum* | Poaceae | Graminoid | X | X | X | | X | X | 57.6 |
| *Paspalum millegrana* | Poaceae | Graminoid | X | X | | X | X | X | 0.7 |
| *Rhynchospora holoschoenoides* | Cyperaceae | Graminoid | X | X | | | X | X | 10.8 |
| *Tabebuia heterophylla* | Bignoniaceae | Tree | X | X | X | X | X | X | 0.4 |
| *Urena lobata* | Malvaceae | Herb | | | | | X | | <0.1 |

Seeds were classified as either bird dispersed or wind dispersed. Landslides where seeds were found are denoted by an X. Dominant landslide cover includes the following: bare (RB12, MY7), climbing fern (ES9, ES17), grass (ES15, ES16).

to perches for each observation period was compared among landslides and among cover class types using Kruskal-Wallis tests. Duration of bird visitation to perches was compared among landslides and among cover classes using one-way analyses of variance (ANOVAs) after homogeneous distributions were determined (two-way ANOVAs could not be used because of lack of replication on one landslide). All statistical analyses were performed using JMP (2000), which expresses critical values in chi-square for the Kruskal-Wallis and Wilcoxon rank scores nonparametric tests. Significance was determined at $p < 0.05$, and means are presented $\pm$ SE.

## Results

A total of 21,507 seeds ($\geq$2 mm) were collected on the six landslides during the 14-month study. Approximately 1%, or 222 seeds, were classified as bird dispersed, and the largest fraction of these (89 seeds) were *Schefflera morototoni*. Most of the wind-dispersed seeds were from two types of grasses, *Andropogon bicornis* and *Paspalum conjugatum* (Table 2). Inputs of bird-dispersed seeds changed seasonally, with most seeds appearing during the wet season (data not shown). When averaged across all six landslides, perch plots had significantly more bird-dispersed seeds than control plots ($\chi^2 = 7.79$; $df = 1$; $p = 0.005$; Fig. 1). Over the course of the 14-month study only two bird-dispersed seeds were found in the control plots within all six landslides. Perches increased seed species richness because 14 of the 28 total species collected were bird dispersed and only found in perch plots, whereas 12 species were wind dispersed and found in both perch and control plots. However, variation among landslides was high with respect to species richness (Table 2).

Although not statistically significant ($\chi^2 = 3.43$; $df = 2$; $p = 0.18$), landslides with grass-dominated ground cover tended to have more bird-dispersed seeds below the perches compared with both climbing fern-covered landslides and bare landslides (Table 3). Additionally, landslides varied widely with respect to wind-dispersed seeds, with the highest number of wind-dispersed seeds on RB12 (Table 3) but with no significant difference among vegetation cover types ($\chi^2 = 3.43$; $df = 2$; $p = 0.18$).

The mean number of seedlings of bird-dispersed seeds

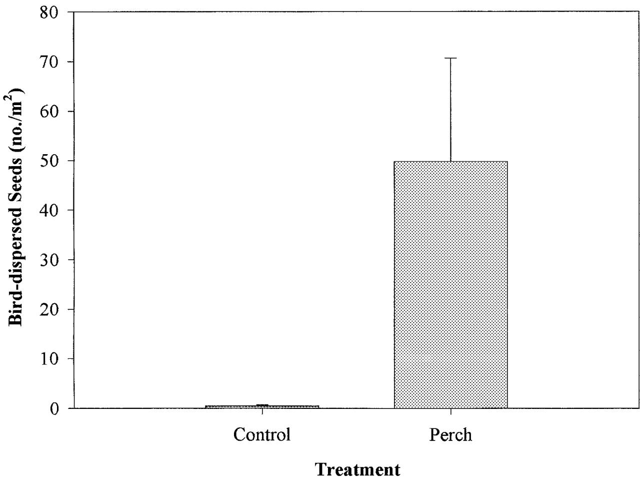



Figure 1. Bird-dispersed seeds per square meter for perch and control plots in six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico (mean ± SE; $n = 6$). The difference between the treatment means is significant ($p = 0.005$).

**Table 4.** Seedlings of bird-dispersed seeds per square meter in perch and control plots on six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico (mean ± SE; $n = 2$ for each site).

| *Site* | *Landslide Cover* | *Perch* | *Control* |
|---|---|---|---|
| RB12 | Bare | 2.58 ± 2.58 | 1.29 ± 1.29 |
| MY7 | Bare | 10.31 ± 7.73 | 0 |
| ES9 | Climbing fern | 0 | 0 |
| ES17 | Climbing fern | 11.60 ± 9.02 | 7.73 ± 0.0 |
| ES15 | Grass | 6.44 ± 1.29 | 0 |
| ES16 | Grass | 0 | 0 |

Means were based on the number of seedlings that established between the first seedling census (when treatments were added) and the final census 13 months later.

that colonized the six landslides was 1.49 ± 1.26 individuals/m$^2$ in control plots and 5.15 ± 2.10 individuals/m$^2$ in perch plots during the 14-month study (Table 4). However, this tendency toward a slightly higher bird-dispersed seedling density beneath perches than controls was not statistically significant ($\chi^2 = 1.87$; $df = 1$; $p = 0.17$).

Twenty-two species of birds, 16 of which consume fruits and/or seeds as part of their diet (Waide 1996), were identified on the six landslides during the bird observation portion of the study. Bananaquits, Black-faced Grassquits, Puerto Rican Emeralds (hummingbirds), and Scaly-napped Pigeons were found at all six landslides. Seven of the 22 bird species were observed on the perches, and six of these seven birds consume fruits and/or seeds as part of their diet (Waide 1996). When the four habitat categories of bird observations were compared on (introduced) perches, on natural perches, on vegetation at the forest edge, or flying over the landslide, birds were most commonly observed perching at the forest edges for all six landslides (Fig. 2).

During the 30 hr of total bird observation at the six landslides, an average of 1.50 birds visited perches per hour, and morning observations of birds on perches (1.46 birds/hr) were similar to afternoon observations (1.67 birds/hr). The average number of visitations to perches varied but was not significantly different among landslides ($\chi^2 = 6.64$; $df = 5$; $p = 0.25$) or vegetation cover types ($\chi^2 = 4.45$; $df = 2$; $p = 0.10$), although bare landslides tended to have the lowest bird visitation to perches. The total number of bird species visiting perches varied among landslides, but overall ES16 had the highest number of bird visitations to perches (Fig. 3A). Black-faced Grassquits were the most common visitors to perches at four of the six landslides, Puerto Rican Tanagers were the only birds observed on perches at landslide ES9, and a single Stripe-headed Tanager was the only observed visitor to perches on the bare landslide MY7 (Fig. 3A). The average time birds occupied perches was 1.10 ± 0.30 minutes per visit. The average time on perches did not differ among landslides ($F = 2.09$; $df = 5$; $p = 0.09$) or cover types ($F = 0.67$; $df = 2$; $p = 0.52$). Puerto Rican Tanagers on landslide ES9 and Gray Kingbirds on ES15 were the two species with the longest duration on the perches (Fig. 3B).

## Discussion

Bird perches increased the abundance, and number of species, of bird-dispersed seeds found on six landslides in the LEF, Puerto Rico. The 14 species of seeds found under

**Table 3.** Bird-dispersed and wind-dispersed seeds per square meter in perch and control plots on six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico (mean ± SE; $n = 2$ for each site).

| | | *Bird-Dispersed Seeds* | | *Wind-Dispersed Seeds* | |
|---|---|---|---|---|---|
| *Site* | *Landslide Cover* | *Perch* | *Control* | *Perch* | *Control* |
| RB12 | Bare | 1.3 ± 1.3 | 0 | 10,297.7 ± 1,019.3 | 7,648.2 ± 5,127.6 |
| MY7 | Bare | 23.3 ± 12.9 | 1.3 ± 1.3 | 39.9 ± 3.9 | 529.6 ± 253.9 |
| ES9 | Climbing fern | 19.3 ± 14.2 | 0 | 37.4 ± 14.2 | 50.3 ± 6.4 |
| ES17 | Climbing fern | 20.6 ± 7.7 | 1.3 ± 1.3 | 56.7 ± 12.9 | 97.9 ± 67.0 |
| ES15 | Grass | 110.8 ± 38.7 | 0 | 2,819.6 ± 667.5 | 1,970.4 ± 14.2 |
| ES16 | Grass | 117.3 ± 64.4 | 0 | 1,662.4 ± 1164.9 | 2,757.7 ± 1,113.4 |

Means were based on 14-month seed totals.

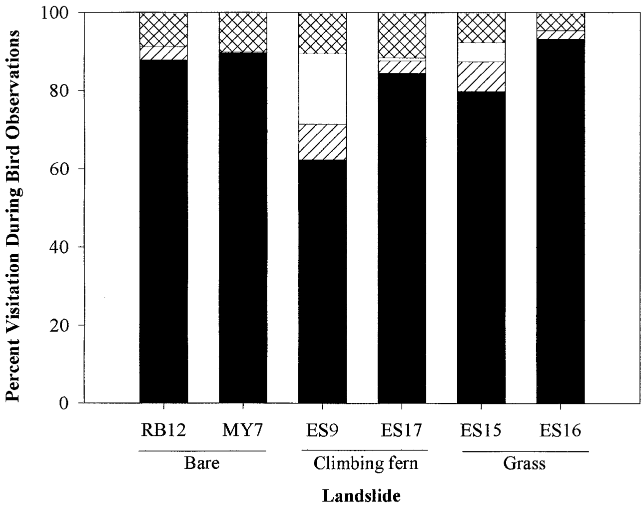
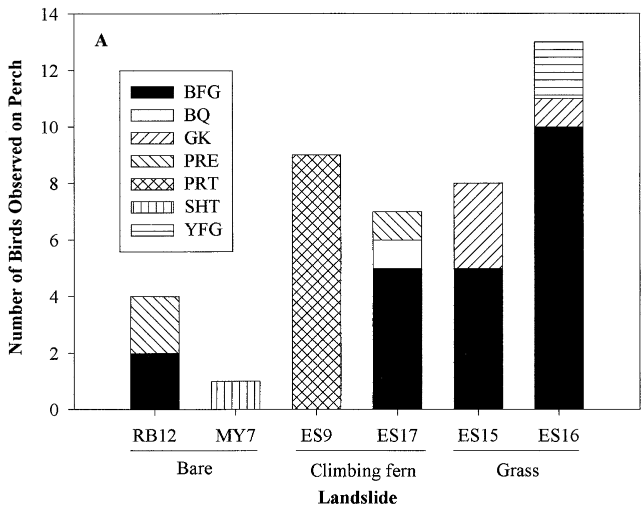



Figure 2. Mean percent visitation of birds observed at each of four locations (solid, forest edge; diagonal, introduced perch; white, natural perch on landslide; cross-hatch, flying) in six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico.



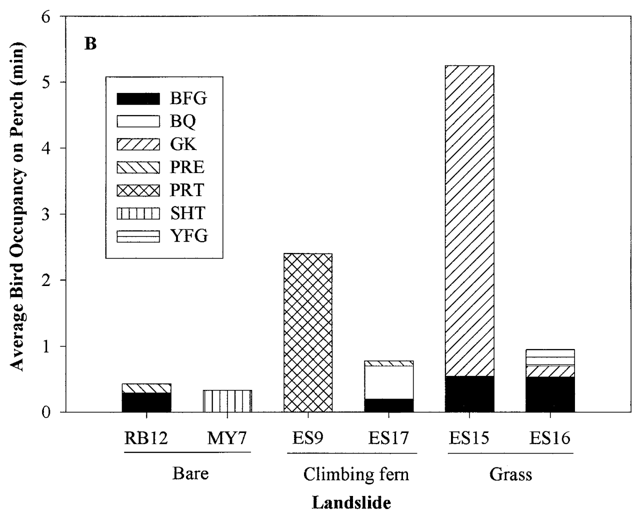




Figure 3. (A) Total number of birds observed on perches and (B) average visitation time (minutes) of birds on perches in the six landslides in the Luquillo Experimental Forest, northeastern Puerto Rico. For each landslide 5 hr (300 minutes) of total observation took place. BFG, Black-faced Grassquit; BQ, Bananaquit; GK, Gray Kingbird; PRE, Puerto Rican Emerald; PRT, Puerto Rican Tanager; SHT, Stripe-headed Tanager; YFG, Yellow-faced Grassquit.

perches that were not found in control plots were tree and shrub species commonly found in mid- to late-successional forests in the LEF. Increasing forest seed deposition to the inner area of these landslides has direct implications for accelerating forest recovery because most of the seeds dispersed into the six landslides were of wind-dispersed early successional origin. Therefore, without perches landslides will experience fewer birds perching that disperse forest seeds, which will likely slow forest recovery on landslides because of the establishment of dominant graminoids and ferns (Walker 1994; Walker & Boneta 1995). Although the 14-month period did not produce significantly more forest seedlings in perch plots than in controls, perches create the possibility of accelerating forest regeneration on landslides in the LEF over the long term if the forest seeds establish.

The rate of seed deposition in this study was high compared with previous studies of disturbed sites in the tropics because seed dispersal (wind + bird) in this study resulted in 11.1 (bare), 5.7 (grass), and 0.2 (climbing fern) seeds/$m^2$/day. The bare and grass habitat variables were higher than seed dispersal (combined wind and animal dispersed) into lowland rainforest treefall gaps in Costa Rica (1.6 seeds/$m^2$/day; Denslow & Gomez Diaz 1990), gaps in the LEF (0.78 seeds/$m^2$/day; Devoe 1989), and forest understory in the LEF (2.55 seeds/$m^2$/day; Devoe 1989). This suggests that bare and grass-covered landslides have higher seed inputs than forests and forest gaps in the LEF. Although Walker and Neris (1993) reported seed rain values (0.3–1.8 seeds/$m^2$/day) from other LEF landslides that more closely resembled LEF gaps and forests, they did not include graminoid seeds. In our study most (99%) seed inputs to landslides were wind-dispersed seeds, and 96% of those dispersed by wind were graminoids. This may help explain why landslides in the LEF are often dominated for decades by grasses and climbing ferns (Walker 1994; Walker & Boneta 1995) and may also justify altering seed dispersal by using perches to increase species diversity and forest seed deposition.

Traps under perches with grass-covered understories tended to have more bird-dispersed seeds than perches with bare soil or climbing fern understories, although a larger sample size would provide a more robust test of this hypothesis. Attraction of birds to perches in the two grass-covered landslides may result from the vegetated ground providing more cover or a better source of food than bare ground (Wunderle 1997). Interestingly, most positive effects of perches increasing seed rain have been found in pastures (McDonnell & Stiles 1983; McDonnell 1986; Holl 1998). To date, only one perch study has shown positive effects with a bare understory (McClanahan & Wolfe 1993). Because tall trees and shrubs promote bird visitation in Puerto Rico (J. Wunderle 2000, U.S. Forest Service, personal communication) and elsewhere (McDonnell 1986; Toh et al. 1999), perches on climbing fern-covered landslides may be less attractive to birds because climbing ferns often reached heights of more than 1.5 m, whereas the grasses were sparser and less than 1 m tall.

Despite an increase in bird-dispersed seeds below perches compared with control plots, there was no significant difference in the presence of forest seedlings after 14 months when perch plots and control plots were compared. This result is similar to that found by Holl (1998) in a 19-month study. Other artificial perch studies did not address this issue (McDonnell & Stiles 1983; McDonnell 1986; Aide & Cavelier 1994) or found only a slight increase in the number of seedlings of bird-dispersed seeds below perches compared with controls after 6 years (1.4–2.0 plants/m$^2$ below perches vs. 0–0.7 plants/m$^2$ in controls; McClanahan & Wolfe 1993). Therefore, the short duration of some studies may be one possibility for the lack of increased forest seedling densities below perches. In addition, the following could have also contributed to the absence of higher seedling densities of bird-dispersed seeds below perches compared with controls: seed loss from predation (rat feces was noted multiple times in and around seed traps), erosion (especially on bare landslides), low soil nutrients (Guariguata 1990; Walker et al. 1996; Shiels 2002), severe microclimate conditions (Walker 1994; Everham et al. 1996; Walker et al. 1996), or competition with preexisting landslide vegetation (Walker 1994; Walker, unpublished data).

Birds frequented the perches more often (approximately 1.5 visits/hr) but stayed perched a shorter duration in this study (approximately 1.10 minutes) when compared with a perch study in a Costa Rican pasture (approximately 0.12–0.41 visits/hr and approximately 3.2 minutes; Holl 1998). The difference between studies may be explained by variation in the distance to the forest edge, because perches were much further from the forest edge in Holl's study (25–250 m) compared with those in our study (5 m). Additionally, most birds in Holl's study were common to the pasture (7 of 10) and not the forest, whereas our study had only 3 of 7 bird species (Black-faced Grassquits, Yellow-faced Grassquits, Gray Kingbird) that were restricted to open areas and not the forest. Therefore, bird species composition and proximity of perches to the forest edge may influence bird visitation to perches, and both of these attributes may affect forest seed dispersal into disturbed areas.

Although perching dispersers include both birds and bats, perching by bats in this study was unlikely. There is only one species of frugivorous bat that frequents the understory at this elevation in the LEF, and it prefers larger perches than used in this study (M. Gannon 2002, Penn State University, personal communication). Only two species of the seeds present beneath the perches (*Clusia clusioides* and *Clusia rosea*) have been documented as being bat dispersed (Willig & Gannon 1996; M. Gannon 2002, personal communication). There was no evidence of bat excrement below perches, but bird excrement (uric acid) was noted on seed baskets and ground cover below perches. Additionally, past observations by several individuals in the LEF (see Devoe 1989) determined that birds, not bats, take the majority of the same seed species as those found below the perches.

Most of the bird species that were observed on perches are considered at least facultatively omnivorous, consuming seeds, fruits, and insects (Waide 1991, 1996) and are capable of dispersing forest seeds onto the landslide or landslide edges. Although Bananaquits are classified as nectivores, this species may be capable of dispersing small-sized seeds (e.g., *Clusia clusioides*, *Miconia*, and *Passiflora*), because fruit, nectar, and invertebrates are common in the Bananaquit's diet (Snow & Snow 1971; Waide 1996). Puerto Rican Tanagers, classified as omnivores, have been noted consuming fruits of similar species as those found below the perches (Waide 1996). Gray Kingbirds are in the flycatcher family but have been known to regularly consume fruits (A. Shiels 2001, personal observation; R. Waide 2001, University of New Mexico, personal communication). Both Puerto Rican Tanagers and Gray Kingbirds likely dispersed forest seeds to perches based on visitation frequency and duration, as well as their larger gape widths compared with most other species observed on perches. Gape sizes of birds usually correlate with fruit and seed sizes they are capable of dispersing (Jordano 2000), and many of the seeds dispersed below perches were larger than 0.5 cm in length (e.g., *Guarea*, *Matayba*, *Myrsine*, *Nectandra*, *Rourea*, *Roystonea*). Such large seeds are likely regurgitated rather than passed through the digestive tract (J. Wunderle 2001, U.S. Forest Service, personal communication). In contrast to the described seed dispersers, it is unlikely that Black-faced Grassquits, Yellow-faced Grassquits, and Puerto Rican Emerald hummingbirds dispersed forest seeds below perches due to their more restrictive diets and smaller gape widths.

Landslides in this study are clearly at different stages of succession. Without perches, bird-dispersed seeds may only enter landslides from the forest edge, thereby contributing to a slow forest recovery. Dense cover of grasses (Holl 1998) and climbing fern (Walker 1994) can make it difficult for seeds to reach the soil (Nepstad et al. 1990; Restrepo & Vitousek 2001) and can inhibit seedling growth due to low light levels and deep litter layers. In this study grass- and fern-covered landslides had less light than bare landslides. However, perches in grass- and fern-covered landslides tended to have a higher bird visitation rate than perches in bare landslides. Therefore, influencing successional trajectories using perches may be most successful on landslides that have enough vegetative ground cover (e.g., grasses and ferns) to attract birds but not enough to inhibit germination of later successional species.

## Conclusion

Additions of perches to landslides increased numbers of bird-dispersed seeds that are of mid- to late-successional origin in the LEF. We were unable to determine why seedling densities of bird-dispersed seeds were not consistently higher beneath perches compared with controls given the greater dispersal of forest seeds below perches, but this could have been the result of insufficient time for a difference to be detected, seed loss from predation, erosion, low soil nutrients, severe microclimate conditions, or competition with preexisting landslide vegetation. Therefore, using perches without any other restoration technique does not accelerate forest recovery on Puerto Rican landslides over a 14-month period. Nevertheless, perch additions to landslides represent a useful and inexpensive management technique for manipulating natural seed dispersal and create the possibility of accelerating the accumulation of a forest seed bank.

Landslide revegetation will occur without additions of bird perches, especially because most seed inputs to landslides are of wind-dispersed origin. However, for forest recovery to occur propagules of mid- to late-successional species must be introduced into landslides. Because few forest species are wind dispersed in the LEF (Devoe 1989; this study) and perches are generally absent after landslides, bird perches provide habitat structure that can be used to accelerate forest seed inputs to landslides. Although promoting forest seed dispersal is a critical step toward accelerating forest recovery, supplemental restoration techniques in addition to bird perches appear to be necessary and should be explored in future studies to increase forest seedling establishment and forest recovery on landslides.

## Acknowledgments

This research was funded by the U.S. Forest Service, University of Puerto Rico, and National Science Foundation supporting the Luquillo Experimental Forest Long-term Ecological Research Program. Additional funding was provided by University of Nevada, Las Vegas International Programs, and Department of Biological Sciences. We thank Laura Weiss, Fred Landau, and Jakob Falk-Sørensen for their helpful field assistance. Special thanks to Maria Aponte for seed collections throughout much of the study. This manuscript was greatly improved by critical review by Mitch Aide, Robert Askins, David Ewert, Daniel Thompson, Diane Wagner, Joe Wunderle, and one anonymous reviewer.

## LITERATURE CITED

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

Augspurger, C. K., and S. F. Franson. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. Journal of Tropical Ecology **4:**239–252.

Brown, S., A. E. Lugo, S. Silander, and L. Liegel. 1983. Research history and opportunities in the Luquillo Experimental Forest. U.S. Forest Service General Technical Report, SO-44, Southern Forest Experimental Station, New Orleans, Louisiana.

Campbell, B. M., T. Lynman, and J. C. Hatton. 1990. Small-scale patterning in the recruitment of forest species during succession in tropical dry forest, Mozambique. Vegetatio **87:**51–57.

Denslow, J. S., and A. E. Gomez Diaz. 1990. Seed rain to tree-fall gaps in a Neotropical rain forest. Canadian Journal of Forest Research **20:** 642–648.

Devoe, N. N. 1989. Differential seeding and regeneration in openings and beneath closed canopy in sub-tropical wet forest. Doctorate dissertation. Yale University, New Haven, Connecticut.

Everham, E. M., R. W. Myster, and E. VanDeGenachte. 1996. Effects of light, moisture, temperature, and litter on the regeneration of five tree species in the tropical montane wet forest of Puerto Rico. American Journal of Botany **83:**1063–1068.

Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the Virgin Islands. U.S. Forest Service Research Paper. ITF-18. Institute of Tropical Forestry, Rio Piedras, Puerto Rico.

Garwood, N. C., D. P. Janos, and N. Brokaw. 1979. Earthquake-caused landslides: a major disturbance to tropical forests. Science **205:**997–999.

Guariguata, M. R. 1990. Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. Journal of Ecology **78:**814–832.

Guevara, S., S. E. Purata, and E. Van der Maarel. 1986. The role of remnant forest trees in tropical secondary succession. Vegetatio **66:**77–84.

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

Janzen, D. H. 1988. Management of habitat fragments in a tropical dry forest: growth. Annual of the Missouri Botanic Garden **75:**105–116.

JMP. 2000. SAS Institute, Incorporated. Cary, North Carolina.

Jordano, P. 2000. Fruits and frugivory. Pages 125–165 in M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. 2nd edition. CABI Publishing, New York.

Larsen, M. C., and A. Simon. 1993. A rainfall intensity-duration threshold for landslides in a humid-tropical environment, Puerto Rico. Geografiska Annaler **75A:**13–23.

Larsen, M. C., and A. J. Torres Sanchez. 1998. The frequency and distribution of recent landslides in three montane tropical regions in Puerto Rico. Geomorphology **24:**309–331.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology **69:**1076–1089.

Little, E. L., R. O. Woodbury, and F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands. Volume 2. U.S. Department of Agriculture, U.S. Forest Service, Washington, D.C.

McDonnell, M. J. 1986. Old field vegetation height and dispersal pattern of bird disseminated woody plants. Bulletin of the Torrey Botanical Club **113:**6–11.

McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia **56:**109–116.

McClanahan, T. R., and R. W. Wolfe. 1993. Accelerating forest succession in fragmented landscapes: the role of birds and perches. Conservation Biology **7:**279–288.

Myster, R. W., and L. R. Walker. 1997. Plant successional pathways on Puerto Rican landslides. Journal of Tropical Ecology **13:**165–173.

Nepstad, D., C. Uhl, and E. A. S. Serrao. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. Pages 215–229 in A. B. Anderson, editor. Alternatives to deforestation: steps toward sus-

tainable use of the Amazon rain forest. Columbia University Press, New York.
Proctor, G. R. 1989. Ferns of Puerto Rico and the Virgin Islands. Memoirs of the New York Botanical Garden. Volume 53. The New York Botanical Gardens, Bronx.
Raffaele, H. A. 1989. Birds of Puerto Rico and the Virgin Islands. Princeton University Press, Princeton, New Jersey.
Restrepo, C., and P. Vitousek. 2001. Landslides, alien species, and the diversity of a Hawaiian montane mesic ecosystem. Biotropica **33:**409–420.
Schemske, D. W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. Ecology **62:**938–945.
Shiels, A. B. 2002. Bird perches and soil amendments as revegetation techniques for landslides in Puerto Rico. MSc Thesis. University of Nevada, Las Vegas.
Slocum, M. G. 2001. How tree species differ as recruitment foci in a tropical pasture. Ecology **82:**2547–2559.
Snow, B. K., and D. W. Snow. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. Auk **88:**291–322.
Soil Survey Staff. 1995. Order 1 soil surveys of Luquillo Long-Term Ecological Research Grid, Puerto Rico. U.S. Department of Agriculture, Natural Resource Conservation Service, Lincoln, Nebraska.
Taylor, C. M. 1994. Annotated checklist of the flowering plants of the El Verde Field Station, Puerto Rico. University of Puerto Rico, Rio Piedras.
Toh, I., M. Gillespie, and D. Lamb. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. Restoration Ecology **7:**288–297.
Waide, R. B. 1991. The effect of Hurricane Hugo on bird populations in the Luquillo Experimental Forest, Puerto Rico. Biotropica **23:**475–480.
Waide, R. B. 1996. Birds. Pages 363–398 in D. P. Reagan and R. B. Waide, editors. The food web of a tropical rain forest. The University of Chicago Press, Chicago, Illinois.
Walker, L. R. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. Journal of Vegetation Science **5:**525–532.
Walker, L. R., and W. Boneta. 1995. Plant and soil responses to fire on a fern-covered landslide in Puerto Rico. Journal of Tropical Ecology **11:**473–479.
Walker, L. R., and L. Neris. 1993. Posthurricane seed rain dynamics in Puerto Rico. Biotropica **25:**408–418.
Walker, L. R., D. J. Zarin, N. Fetcher, R. W. Myster, and A. H. Johnson. 1996. Ecosystem development and plant succession on landslides in the Caribbean. Biotropica **28:**566–576.
Wiley, J. W., and G. P. Bauer. 1985. Caribbean National Forest, Puerto Rico. American Birds **39:**12–18.
Willig, M. R., and M. R. Gannon. 1996. Mammals. Pages 399–433 in D. P. Reagan and R. B. Waide, editors. The food web of a tropical rain forest. The University of Chicago Press, Chicago, Illinois.
Willson, M. F., and F. H. J. Crome. 1989. Patterns of seed rain at the edge of a tropical Queensland rain forest. Journal of Tropical Ecology **5:** 301–308.
Wunderle, J. M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. Forest Ecology and Management **99:**223–235.
Wunderle, J. M., A. Diaz, I. Velazquez, and R. Scharrón. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. Wilson Bulletin **99:**22–37.
Young, K. R., J. J. Ewel, and B. J. Brown. 1987. Seed dynamics during forest succession in Costa Rica. Vegetatio **71:**157–173.