

Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal

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Abstract. Regenerated forests now compose over half of the world's tropical forest cover and are increasingly important as providers of ecosystem services, freshwater, and biodiversity conservation. Much of the value and functionality of regenerating forests depends on the plant diversity they contain. Tropical forest diversity is strongly shaped by mutualistic interactions between plants and fruit-eating animals (frugivores) that disperse seeds. Here we show how seed dispersal by birds can influence the speed and diversity of early successional forests in Puerto Rico. For two years, we monitored the monthly fruit production of bird-dispersed plants on a fragmented landscape, and measured seed dispersal activity of birds and plant establishment in experimental plots located in deforested areas. Two predominantly omnivorous bird species, the Northern Mockingbird (*Mimus polyglottos*) and the Gray Kingbird (*Tyrannus dominicensis*), proved critical for speeding up the establishment of woody plants and increasing the species richness and diversity of the seed rain in deforested areas. Seed dispersal by these generalists increased the odds for rare plant species to disperse and establish in experimental forest-regeneration plots. Results indicate that birds that mix fruit and insects in their diets and actively forage across open and forested habitats can play keystone roles in the regeneration of mutualistic plant–animal communities. Furthermore, our analyses reveal that rare-biased (antipostatic) frugivory and seed dispersal is the mechanism responsible for increasing plant diversity in the early-regenerating community.

Key words: antipostatic; diversity-maintenance mechanism; fruit choice; mutualisms; negative density dependence; negative frequency dependence; nucleation; secondary succession; seed dispersal networks; tropical forests.

INTRODUCTION

Secondary forests now compose over half of the world's tropical forest cover and are increasingly important as providers of ecosystem services, freshwater, and conservation of biodiversity (Chazdon 2014). Much of the value and functionality of secondary forests depends on the plant diversity they contain, with higher diversity being associated with increased provision of ecosystem services (Isbell et al. 2011). In turn, tropical forest diversity is strongly shaped by mutualistic interactions between plants and fruit-eating animals (frugivores) that disperse seeds (Terborgh et al. 2002, Bascompte and Jordano 2007, Chazdon 2014). Frugivores affect the potential of forests to regenerate in both deforested (Guevara et al. 1986, Holl 1999) and forested sites (Terborgh et al. 2011, Chazdon 2014). Ultimately, frugivores are believed to influence the capacity of plant species to coexist (Rohr et al. 2014). But field experiments testing how frugivory and seed dispersal affect plant community structure and assembly are lacking. Furthermore, the specific

mechanisms involved in plant diversity maintenance by frugivores remain speculative or unknown.

Seed dispersal into cleared lands plays a crucial role in secondary forest succession (Aide and Cavellier 1994, Holl 1999) and provides the initial templates that influence the assembly and diversity of novel forests (Wunderle 1997). Here we considered the early stages of forest regeneration as a setting to investigate how bird frugivory and seed dispersal processes shape forest regeneration and community diversity. We conducted a field experiment to compare seed dispersal and plant establishment in experimental patches where birds dispersed seeds, to patches from which birds were excluded (Fig. 1). We assessed the effects of bird frugivory and dispersal on the diversity of the regenerating community by comparing seed availability in the landscape with seed arrival and recruitment in the experimental plots. We focused on birds because they are dominant frugivores in most terrestrial ecosystems (Jordano 2000). In Puerto Rico alone, bird-dispersed trees account for ~75% of all tree and shrub species including most of the dominant species in secondary forests across the island (Carlo et al. 2003). Our null expectation was that seed dispersal by birds is a random process driven by the availability of seed within fleshy fruits on the landscape (i.e., frugivores make

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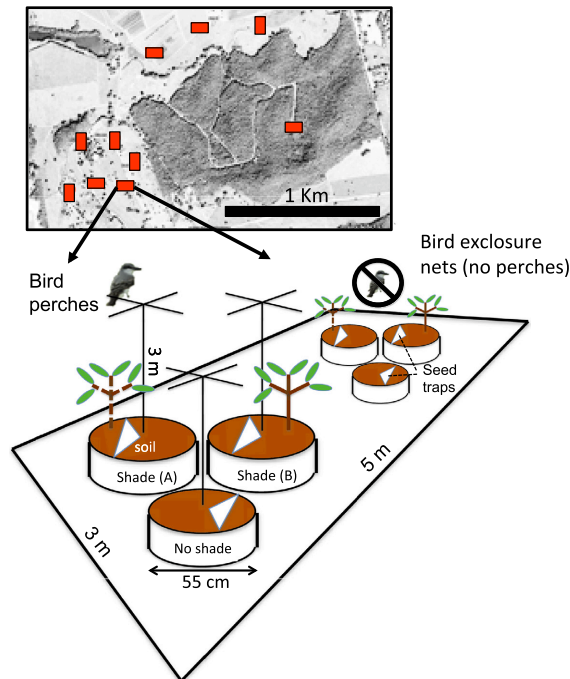


FIG. 1. Overview of plot setup in Finca Montaña, north-western Puerto Rico ($18^{\circ}28'03.00''$ N; $67^{\circ}06'46.97''$ W). Ten plots were constructed in open pastures at varying distances from fragments of moist karstic tropical forest. Soil patches with different shade types (no shade, artificial shade, and shade by sapling of *Spathodea campanulata*) were paired according to a “bird” treatment (with perches) and a “no-bird” treatment (without perches and with nets to exclude birds). One of the plots was located in a small clearing (~ 2 ha) within the secondary forest patch (plots not drawn to scale on map). See *Methods* and Appendix S1 figures for more detail.

proportional use of fruit resources). Alternatively, frugivorous birds could alter the representation of plant species in the seed rain through fruit selection and biased movement between forested and deforested areas that lead to seed dispersal events (Carlo and Yang 2011).

Fruit selection can take several forms. At the most elemental level, birds choose to eat species available in the community based on matching fruit and bird traits (Jordano et al. 2003, González-Castro et al. 2015). When species traits do not forbid interactions from happening, relative abundance of fruiting species can be a strong predictor for interaction frequencies (Carlo et al. 2003). For example, the relative abundance of fruiting species can generate frequency-dependent selection in either positive (*apostatic*) or negative (*antiapostatic*) fashion (Allen and Greenwood 1988, Allen and Weale 2005). Apostatic frugivory would result in an over-representation of common fruiting species in the seed rain, increasing their dominance and negatively affecting community diversity. On the other hand, antiapostatic selection would increase the representation of rare species in the seed rain (hereafter *rare-biased* dispersal) and thus increase community diversity.

Negative frequency- and density-dependent processes that operate via interference and antagonistic plant–animal

and plant–plant interactions are recognized as key processes that increase the coexistence capacity of species and thus maintain community diversity (Janzen 1970, Chesson 2000, Terborgh 2012). Yet, we know of no previous study showing or suggesting that seed dispersal in a community context can be actively modulated by frugivores in a way that is parallel to recognized Negative Density-Dependent (NDD) mechanisms. Here we show that omnivorous birds that feed on a wide variety of fruit contribute to forest regeneration in two ways: by accelerating the establishment of woody vegetation in deforested areas, and by increasing the plant community diversity via rare-biased seed dispersal.

METHODS

Study site

The study was conducted at Finca Montaña, municipality of Aguadilla, Puerto Rico ($18^{\circ}28'03.00''$ N; $67^{\circ}06'46.97''$ W). The location is administrated by the College of Agriculture of the University of Puerto Rico at Mayagüez and is dedicated exclusively to research and conservation. The study landscape consists of 240 ha of managed cattle pastures (including an area of soy and corn fields) and 190 ha of secondary forests >50 yr old. There are six forest fragments, four small (1–3 ha), and two large (100 and 87 ha; Appendix S1: Fig. S1). Annual rainfall at the site averages 100–125 cm per year. Rainfall occurs in any month, but typically there is a February–May dry season averaging <8 cm/month, and a wetter season in August–November with an average precipitation range of 15–20 cm/month. Vegetation is classified as subtropical moist karstic forest (Aukema et al. 2007).

Setup of experimental plots

In August of 2010, we established 10 experimental plots (Fig. 1) in open pastures actively grazed by cattle to measure bird activity, the seed rain, and plant establishment. Plots were located at a nearly uniform range of distances from forest edges: 20, 25, 38, 50, 95, 125, 145, 154, 196, and 240 m. At this scale, distance to forest edge did not have a significant effect on the density or species richness of the seed rain during the sampling period (Appendix S1: Fig. S2, see also Laske and Keitt 2012). To set up a plot, we first leveled the surface with a bulldozer to remove existing vegetation, topsoil, and roots. No roots or stems were left to prevent plants establishment by resprouting. Each experimental plot measured 3×4 m and was fenced with barbed wire to keep cattle out. Within the fenced enclosure, we placed six plastic rings (hereafter the experimental patches) built by assembling three pieces of flexible plastic edging (Easy Edging, Progressive Global Enterprises, Birmingham, Alabama, USA) into a ring measuring 55 cm in diameter (0.24 m², Fig. 1). Half of the patches in each plot were covered with a net to exclude birds (Fig. 1). Rings raised ~ 10 cm from the soil surface (Appendix S1: Fig. S3). To

start the experiment, we filled the patches with soil (a local Oxisol, Eustrustox, Coto series) extracted from the B-horizon at depths of 0.25–0.5 m. For this we used a 1.5 m deep, 1 m wide trench that was dug with a bulldozer in the study site. Before adding it to the experimental patches, we thoroughly mixed the soil to homogenize the material. Using soil extracted from the B-horizon (30–70 cm deep) ensured that the soil was seedless at the start of the experiment. We note that using material from the B-horizon likely created tougher-than-natural conditions for seed germination and establishment (i.e., as compared to top soil).

We controlled seed predation in order to minimize the effects of post-dispersal processes on recruitment. To keep rodents out, we covered the patches with hardware mesh (1 × 1 cm). This mesh size was large enough to allow almost all bird-dispersed seeds in the community to go through and reach the soil of the experimental patches (Appendix S1: Fig. S3). The steel mesh remained in place for the first 9 months of the experiment before removing it to allow vegetation to grow unconstrained. To control ants, we maintained a ring of Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan, USA) to the outside of the plastic rings.

In the center of bird treatment patches, we installed a 3 m tall steel pipe (2.5 cm in diameter) with two perpendicular wooden rods (25 cm long × 0.75 cm in diameter) that served as bird perches on the top (Appendix S1: Fig. S3). A triangular seed trap (25 × 25 × 35 cm; area = 0.03 m²) made of steel mesh and lined with nylon fabric was used to sample the seed rain (Appendix S1: Fig. S3). All patches were open to other forms of seed dispersal (e.g., wind and bat, but note that frugivorous phyllostomid bats commonly defecate while flying over open fields; see Charles-Dominique 1986). Seeds were collected from the seed traps at least once a month and identified using a reference collection for the site. After identification and counting, seeds were added to the soil patch where found (i.e., non-destructive sampling).

Within bird and no-bird treatments, there were three types of patches: one patch had no shade, another was shaded with plastic leaves, and in the last we planted a small sapling of *Spathodea campanulata* (0.25–0.3 cm in height at the moment of planting). Our rationale was again to minimize the effects of post-dispersal process by provide abiotic heterogeneity to maximize establishment of different species (i.e., species that prefer shaded microhabitats or not). We chose *S. campanulata* to use as the “natural” nursing shade because it is the most abundant early successional tree species in Puerto Rico (Lugo 2004). Patches with plastic leaves provided a nursing shade without the belowground or aboveground effects of a live nurse tree like *S. campanulata* plant.

Measuring plant recruitment in experimental patches

In September of 2012, two years after the start of the experiment, we tallied, identified to the lowest possible

taxonomic level, and measured (height and width) all plants growing in the experimental patches. For grasses and non-ornitochorous plants, we recorded their cumulative cover on the experimental patches.

Measuring the abundance of reproductive bird-dispersed plant species on the landscape

We obtained landscape-level densities of reproductive fleshy-fruited plants (i.e., trees, shrubs, vines, herbs, mistletoes) from 10 100 × 2 m transects established haphazardly in forest patches, two 100 × 2 transects along forest edges, two vegetated fence lines, and six 100 × 100 m pasture plots (Appendix S1: Fig. S1). The larger square plots used in open pastures were necessary to tally fleshy-fruited plants growing along fence lines and scattered on pastures. The total area sampled was pasture + edge + forest plots = 62,600 m². A rarefaction analysis shows that sampling was adequate to detect the bulk of the plant species on the study landscape (Appendix S1: Fig. S4). The six most abundant canopy tree species were *Bursera simaruba*, *Coccoloba diversifolia*, *Krugiodendron ferreum*, *Citharexylum spinosum*, *Sideroxylon salicifolium*, and *Eugenia monticola*. A full list of plant species, families, and fruit characteristics is shown in Appendix S1: Table. S1.

Quantifying monthly seed densities of ornitochorous species in the plant community

We counted fruits at the start of each month on a sample of 163-tagged adult plants (trees, shrubs, lianas, and mistletoes) representing 41 ornitochorous species (Appendix S1: Table. S1). For each species, up to 10 adult individuals were tagged, although the final sample size for each species reflected their relative abundance in the community. This resulted in 60% of the species in the sample having at least three tagged individuals (3.5 ± 0.33 , mean \pm SE), while 40% of species was limited to one or two individuals because of their rarity. For large trees with thousands of fruits, we counted fruits in three to four representative branches and then extrapolated to the rest of the canopy area bearing fruit, but when possible (e.g., small plants or small fruit crops) we counted all fruits without extrapolating.

We estimated the landscape-level seed availability using bootstrap samples for all plant species for which at least one individual was detected with ripe fruit each month. Bootstraps (as opposed to simple averages) were used to account for the variability in seed availability given by both the spatial distribution of plants and the variance in seed production of individual plants. For every plant species, we sampled with replacement the number of individuals per hectare from the 20 vegetation census plots (note that density estimates varied from plot to plot). Each bootstrap sample served to determine the size of the associated sample of fruits per plant from the phenology data every month. For

example, if the b th sample drawn for a particular species was 10 individuals/ha, we then took a sample (with replacement) of size 10 from the list of fruits per individual recorded that month. These values were then transformed to number of seeds by multiplying the sampled number of fruits by the average number of seeds per fruit for the species. For every month and plant species, we obtained 10^4 bootstrap samples that we used to estimate average and 95% percentiles of landscape-level seed availability.

Bird activity in plots

We used digital video cameras to sample bird activity on the perches of the experimental plots (Appendix S1: Fig. S3, panel A). One day each week, a tripod-mounted camera (Samsung SMX F-40, South Korea) was deployed in every plot during the early morning (07:00–08:00 h) and recorded for ~300 min until the battery ran out (299.8 ± 11.9 min, mean \pm SE). Rainy days were avoided since cameras were not weather proof. From the footage, we extracted the time (in seconds) and the number of times that each bird species was recorded on the perches (visits). Visitation time and total visits per species were positively correlated ($r^2 = 0.90$, $P < 0.0001$), but for analysis we use the cumulative number of visits because birds could spend much time on a perch only occasionally, while visitation to perches can be expected to be more directly linked to movements, and thus, to different foraging and seed dispersal events.

Frugivore movements between open and forested habitats

During the months of May and June 2011, we observed 285 bird movements (flights) from 11 bird species in the community, noting whether they took place between open areas and forested areas. We observed habitat crossovers of bird species by walking along the boundaries of forest patches and pastures. We compared the frequency of crossovers among bird species in the community.

Bird abundance

To estimate the relative abundance of bird species on cleared lands we conducted 5-min point counts at the experimental plots in the cleared habitats (Appendix S1: Fig. S1). Six point count stations were also established in the forest fragments (Appendix S1: Fig. S1). We conducted a total of 12 point counts, one each month during 2010–2011 starting in September. A census of all stations (forest and pasture) was conducted in a single morning between 06:30 and 09:30. A local bird expert (Sergio A. Colón-López) conducted all counts following a fixed order to visits the census stations every time, but rotating the start point on each day to prevent time biases. Relative detections (first averaged across months, then across point count stations) are shown in Appendix S1: Table S2.

Feeding records

Once a month from February to November 2013, and in June–July 2014 we obtained frugivory records by conducting systematic walks that traversed through forest and pasture areas of the study landscape. Observations took place in the morning hours (07:00–10:00) and the bearing and start point of transects were randomly chosen. A single experienced observer collected 649 independent (i.e., non-sequential, sensu Carlo et al. 2003) frugivory records. The identity of the bird species and the food item (i.e., fruiting species, insect, etc.) was noted in each case.

Statistical analyses

Effects of birds on seed rain and plant establishment in experimental plots.—We first used a MANOVA to examine the effects of the bird perch treatments on the seven response variables before analyzing them separately in univariate fashion: average number of bird-dispersed seeds per plot, average number of wind-dispersed seeds per plot, average number of trees, shrubs and vines, mean percent cover of grasses, and mean vegetation volume. The MANOVA model was significant (exact $F = 9.80$, numerator $df = 6$, denominator $df = 10$, $P = 0.001$), thus we followed with univariate post hoc paired t tests for each response (Fig. 2). We also compared recruitment by shade type (microhabitat: no shade, artificial shade, and shade by *S. campanulata*, Fig. 1) using the same approach. The only difference is that for microhabitat recruitment analyses, we used data from an earlier vegetation census conducted in the experimental patches in July 2011 because after that point, plant growth was blurring the initial microhabitat conditions. Analyses were done in JMP Pro (11.02, SAS Institute, Cary, North Carolina).

Relationship between seed availability, seed dispersal, and recruitment at the community scale.—We fitted seed dispersal and recruitment as a function of the average fruit abundance of each plant species' using least square regression. Only plant species for which fruit abundance data was available were used in these analyses (i.e., rare species shown as open bars in Fig. 3 are excluded from statistical analyses). We also calculated diversity (Shannon's H') and evenness (Pielou's J) using average values for plant species of fruit abundance, seed dispersal, and recruitment, as calculated across the ten experimental units (Fig. 3). Very rare species for which we have no phenology data (open bars, Fig. 3) were also excluded from diversity and evenness metrics. From this and other analyses (*Assessing rare-biased (antiapostatic) seed dispersal*), we excluded two of the original 41 plant species for phenology, *Ficus citrifolia* and *Tetrazygia elaeagnoides*, because their seeds were too small and were not retained well by our seed traps.

Assessing rare-biased (antiapostatic) seed dispersal.—We examined whether seed dispersal was higher than expected, as expected (random), or lower than expected

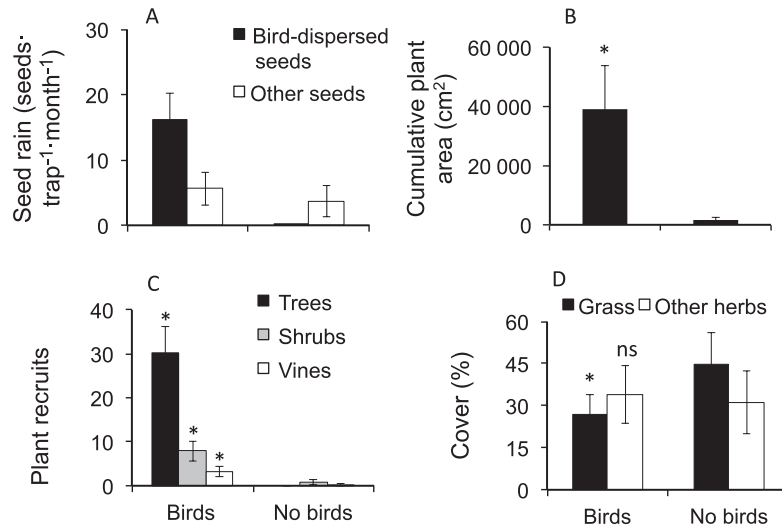


FIG. 2. (A) Patches with birds had a more diverse and dense seed-rain-dominated bird-dispersed plant species (black bars, paired $t = 3.57$, $df = 18$, $P = 0.0022$) than patches without birds (open bars, paired $t = 0.85$, $df = 18$, $P = 0.407$). (B) Total plant growth was more than an order of magnitude higher in plots with birds (paired $t = 2.18$, $df = 18$, $P = 0.0427$). (C) After 2 yr, bird patches had more saplings of trees (black bars, paired $t = 6.05$, $df = 18$, $P = 0.0012$), shrubs (gray bars, paired $t = 3.69$, $df = 18$, $P = 0.0017$), and vines (open bars, paired $t = 3.59$, $df = 18$, $P = 0.0021$). (D) In contrast with plots with birds, grasses and herbs dominated patches without birds, showing arrested regeneration (grasses paired $t = 6.09$, $df = 18$, $P < 0.0001$). All bars show the simple raw means (\pm SE) with no pair centering.

by plotting, for each plant species, the monthly proportion of seeds found in the seed rain (seed counts summed across seed traps of the 10 experimental plots) against the proportion that the species represented that month in the community as calculated from the phenology and plant species' abundances. To estimate the expected proportion of a particular species in the seed traps for the of birds dispersing seeds at random, we sampled from each of the 10^4 bootstrap estimates of landscape-level seed abundance (see *Quantifying seed densities of fleshy-fruited species in the plant community* above) a number of seeds equal to the observed number of dispersed seeds in the experimental plots. From these samples, we obtained the 95% intervals for the proportion of expected dispersed seeds for every plant species. If the observed proportion was above these values, the focal species was dispersed more than just by chance alone (i.e., preference). On the contrary, if the observed proportion was below the 95% interval, the species was dispersed less than expected (i.e., avoidance).

We conducted a multinomial ordinal logistic regression to examine how relative seed dispersal of plant species was related to seed relative availability in the community. For this, we used as the response variable the classification of the monthly proportion of dispersal for the 25 plant species with at least 7 months of data as determined by the bootstrapping procedure explained above (i.e., higher than random, random, less than random). As explanatory variables we used the proportion of seed abundance (per month) and the species identity. This analysis is a simple way to examine apostatic or antiapostatic seed dispersal as it models how relative resource abundance relates to

the cumulative probability of detecting dispersal that is disproportionately high, random, or disproportionately low for plant species in the community.

Correlation between seed rain and bird perching activity.—We used least square regression to fit the number of seeds (log-transformed to meet normality assumption) and the species richness (counts met normality assumption without transformation) of the seed rain on experimental plots as a function of the perching activity (total number of visits) of Mockingbirds and Kingbirds using least square regression (JMP Pro 11.2). After finding no traces of an interaction between Mockingbird and Kingbird visits at experimental plots (Mockingbird visits \sim Kingbird visits; $r^2 = 0.016$, $P = 0.72$) we considered the activity of Mockingbirds and Kingbirds as a single explanatory variable since these two species were the most important frugivores in the community, and no other bird species spent significant time on the perches, and the activity of all other species shows no trend in relation to the seed rain (Table 1).

Bird abundance, inter-habitat movements, and frugivory network.—Census data on the bird community was analyzed by ordination of census points based on the average detections of bird species (across months) using nonmetric multidimensional scaling in R (version 3.02) with the vegan package (2.0). Movements between open and forested habitats of bird species with seed dispersal capabilities (Table 1) were compared using a contingency table analysis. For this we calculated, for each species, the proportion of all movements that were classified as crosses between open and forested hab-

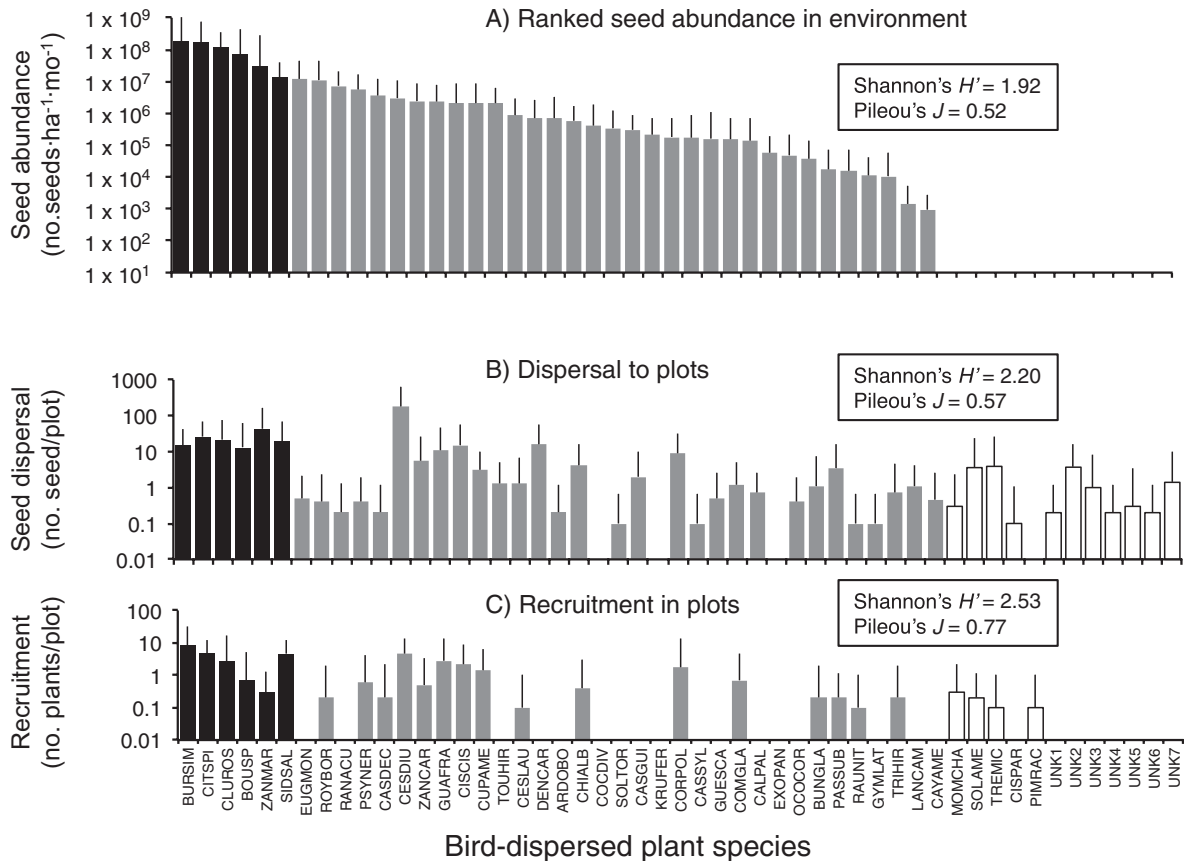


FIG. 3. Plant species dispersed by birds in the community, rank-ordered by average seed abundance (within fleshy fruits) on the landscape. Black bars show six species that altogether produced >95% of all seeds. White bars are rare bird-dispersed species that were present in the seed rain/recruitment but were absent from vegetation surveys and lacked seed abundance data (these include seven unidentified species shown, but not used in diversity calculations or statistical analyses). Notice that frugivory increased the diversity and evenness of the seeds of the plant community during dispersal, a process that made the community of seedlings more equal and diverse. Species abbreviations: BURSIM, *Bursera simaruba*; CITSPI, *Citharexylon spinosum*; CLUROS, *Clusia rosea*; BOUSP, *Bourreria* spp.; ZANMAR, *Zanthoxylon martinicensis*; SIDSAL, *Sideroxylon salicifolium*; EUGMON, *Eugenia monticola*; ROYBOR, *Roystonea borinquena*; RANACU, *Randia aculeata*; PSYNER, *Psychotria nervosa*; CASDEC, *Casearia decandra*; CESDIU, *Cestrum diurnum*; ZANCAR, *Zanthoxylon caribaeus*; GUAFRA, *Guapira fragrans*; CISCIS, *Cissus cissyoides*; CUPAME, *Cupania americana*; TOUHIR, *Tournefortia hirsutissima*; CESLAU, *Cestrum laurifolium*; DENCAR, *Dendropemon caribaeus*; ARDOBO, *Ardisia obovata*; CHIALB, *Chiococca alba*; COCDIV, *Coccoloba diversifolia*; SOLTOR, *Solanum torvum*; CASGUI, *Casearia guianensis*; KRUGFER, *Krugiodendron ferreum*; CORPOL, *Cordia polycephala*; CASSYL, *Casearia sylvestris*; GUESCA, *Guettarda scabra*; COMGLA, *Comocladia glabra*; CALPAL, *Calyptantes pallens*; EXOPAN, *Exothea paniculata*; OCOCOR, *Nectandra coriacea*; BUNGLA, *Bunchosia glandulosa*; PASSUB, *Passiflora suberosa*; RAUNIT, *Rauwolfia nitida*; GYMLAT, *Gyminda latifolia*; TRIHIR, *Trichilia hirta*; LANCAM, *Lantana camara*; CAYAME, *Cayaponia americana*; MOMCHA, *Momordica charantia*; SOLAME, *Solanum americanum*; TREMIC, *Trema micrantha*; CISPAR, *Cissampelos pareira*; PIMRAC, *Pimenta racemosa*.

itats. To evaluate the relative importance of birds as frugivores in the community we constructed a bipartite network (R v. 3.2.1, package bipartite v. 2.04) using an adjacency matrix of bird species \times plant species and the number of frugivory records for each bird–plant species pair as weights.

RESULTS

Seed rain

We found 4,216 seeds in the experimental seed traps during the two years of study. Of these, 96.12%

belonged to 53 ornithochorous plant species (Fig. 3B, Appendix S1: Table S1), and 3.82% belonged to wind-dispersed seeds from at least three species of Poaceae. A rarefaction curve analysis shows that the 10 experimental plots were able to capture the majority of the community of seeds that birds were dispersing in the open habitats (Appendix S1: Fig. S5). Nearly all dispersed seeds were found in traps under bird perches while the few found in seed traps without bird perches were from grasses and herbs (Fig. 2A). Under perches we detected dispersal of 86% of the ornithochorous plant community (Fig. 3B), while patches with bird exclosures received no ornithochorous species (Fig. 2A).

TABLE 1. Summary of cumulative bird activity on the perches of experimental plots (averaged across the 10 experimental units) and the relative detections from point counts (averaged across months, then across experimental units) in pastures and forest.

Bird species	Dietary guild	Perching time (sec)	No. plots detected	Detections in pastures	Detections in forest
<i>Mimus ptyglossus</i>	insectivore–frugivore	6071.7 ± 1658.9	10	0.55 ± 0.07	0.07 ± 0.04
<i>Tyrannus dominicensis</i>	insectivore–frugivore	5832.2 ± 1175.8	10	0.43 ± 0.08	0.12 ± 0.06
<i>Tiaris bicolor</i>	granivore	1047.8 ± 504.	9	1.28 ± 0.17	1.00 ± 0.17
<i>Falco sparverius</i>	raptor	556.4 ± 472.1	3	0.01 ± 0.14	0
<i>Columbina passerina</i>	granivore	226.6 ± 202.1	4	0.28 ± 0.09	0.14 ± 0.05
<i>Quiscalus niger</i>	insectivore	198.4 ± 194.2	2	0.31 ± 0.18	0.05 ± 0.05
<i>Tiaris olivacea</i>	granivore	151 ± 105.2	3	0.70 ± 0.11	0.07 ± 0.05
<i>Zenaida asiatica</i>	granivore	70.8 ± 37.9	1	0.01 ± 0.01	0
<i>Zenaida aurita</i>	granivore	68.6 ± 68.6	3	0.36 ± 0.12	0.26 ± 0.10
<i>Icterus icterus</i>	insectivore/nectarivore	19.4 ± 14.2	2	0.03 ± 0.02	0
<i>Euplectes orix</i>	granivore	17 ± 14.3	3	0.04 ± 0.03	0
<i>Vidua macroura</i>	granivore	13.8 ± 13.8	1	0.01 ± 0.01	0
<i>Crotophaga ani</i>	insectivore	0	0	0.13 ± 0.01	0
<i>Vireo altiloquous</i>	insectivore–frugivore	0	0	0	0.36 ± 0.08
<i>Turdus plumbeus</i>	frugivore–insectivore	0	0	0	0.19 ± 0.06
<i>Margarops fuscatus</i>	insectivore–frugivore	0	0	0	0.07 ± 0.04
<i>Patagioenas squamosa</i>	frugivore	0	0	0	0.15 ± 0.06
<i>Spindalis portoricensis</i>	frugivore	0	0	0	0.92 ± 0.14
<i>Euphonia musica</i>	frugivore	0	0	0	0.01 ± 0.01
<i>Loxigilla portoricensis</i>	frugivore	0	0	0	0.63 ± 0.13
<i>Geotrigon chrysis</i>	granivore–frugivore	0	0	0	0.11 ± 0.06

Notes: Abbreviations are FI, frugivore–insectivore (i.e., more frugivorous than insectivorous), F, frugivore; I, insectivore; IF, insectivore–frugivore (i.e., more insectivorous than frugivorous); G, granivore; GF, granivore–frugivore; R, raptor. Values are mean ± SE.

Bird-dispersed woody species (trees and shrubs) dominated the seed rain (Fig. 2B). The largest quantity of seeds belonged to the shrub *Cestrum diurnum* (42.78%), followed by seeds of the trees *Zanthoxylon martinicensis* (10.58%), *Citharexylum spinosum* (6.35%), and *Clusia rosea* (5.08%). The ornitochorous seed rain included 1.6% from seven morphospecies, three of which were as abundant (or more) in the seed rain than seeds of several common species (Fig. 3B and C). The cumulative number of plant species reaching an experimental patch with perches after two years ranged between 15 and 36 (24.5 ± 2.12 , mean ± SE). Thus, about one-half of the ornitochorous species in the community were represented in the average seed rain of patches with perches after two years (Appendix S1: Fig. S6).

The bird-generated seed rain and relationships to seed availability

Seed availability of ornitochorous plants was dominated by six species that collectively accounted for over 90% of the seed production: *B. simaruba*, *C. spinosum*, *C. rosea*, *Bourreria* spp. (this includes *B. virgata* + *B. succulenta* due to nearly indistinguishable fruits and seeds), *Zanthoxylon martinicensis*, and *S. salicifolium* (Fig. 3A). All of these species were among the most common canopy species in the forest patches (Appendix S1: Table S1), and were also common as scattered

individual trees in open pastures and along their fence lines.

When comparing the availability of plant species' seeds (monthly averages) with the number of those seeds arriving to experimental plots we find that they were positively correlated, even more strongly if the small-seeded *C. diurnum*, the most common species in the seed rain, were excluded from scatterplots (Appendix S1: Fig. S7). Still, availability was not as strong a predictor of dispersal since too many species of low seed availability in the community experienced high relative dispersal (Fig. 3B). When examining the diversity (Shannon's *H'*) and evenness (Pielou's *J*) of the community of bird-dispersed seeds we found that they were both higher than in the estimates of seed availability (Fig. 3A and B).

Analysis of the monthly proportions that each plant species composed of the bird-generated seed rain as a function of their proportion of that month's seed availability in the community shows that rare-biased and antiapostatic dispersal was common (Fig. 4). For example, seeds of the most abundant species, *B. simaruba* (BURSIM), were never dispersed more than expected by chance but were dispersed less than expected in most months of high relative abundance (Fig. 4A). Common species like *C. rosea* (CLUROS) and *S. salicifolium* (SIDSAL), had a clear antiapostatic pattern of dispersal: seeds dispersed in larger quantities when fruits were proportionally rare, and dispersal was less than expected when proportionally more abundant in the community

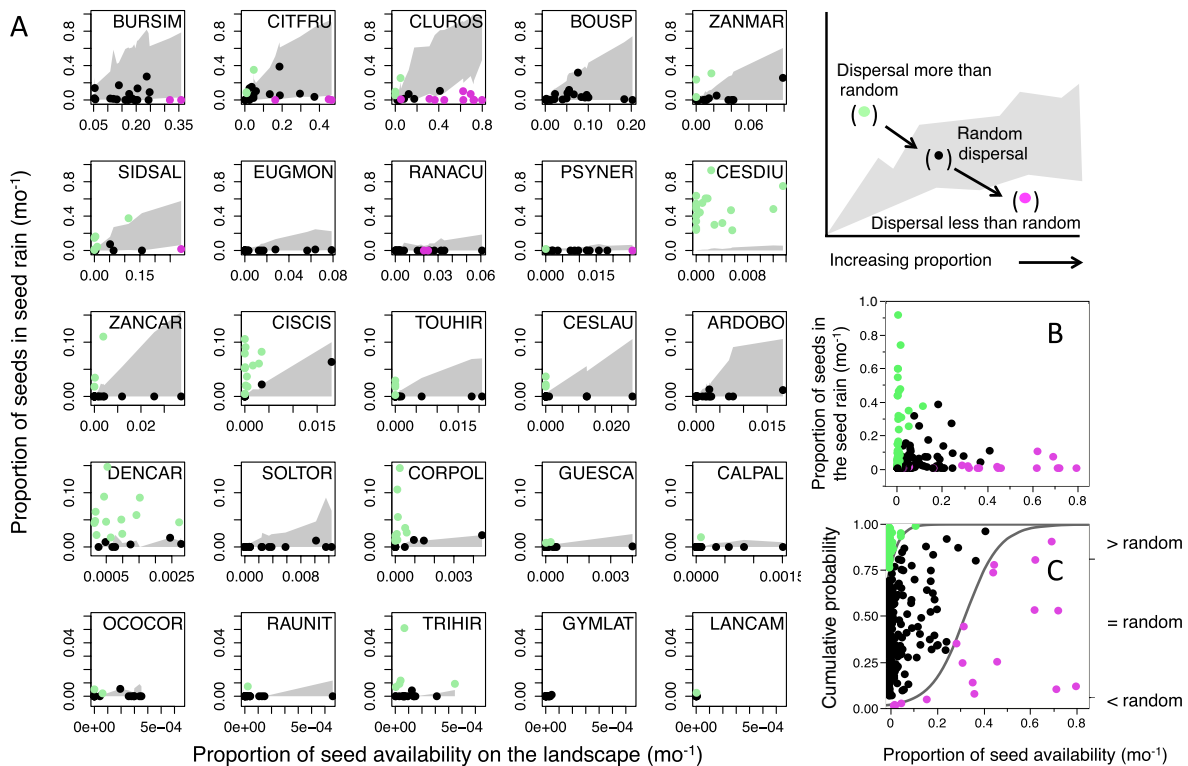


FIG. 4. Scatterplots (A) relating the proportion of monthly seed abundance (within fruits) for 25 plant species (x -axis) with the proportion of seeds found in the bird-generated seed rain at experimental plots (y -axis). Plots show plant species with at least 7 months of data ordered from most abundant (top left) to least abundant (bottom right). As explained in the panel at the top right, probability of dispersal by birds was significantly higher than random (green dots) for species when points lie above shaded areas, and significantly lower below the shaded areas (magenta dots). Shaded areas are confidence intervals representing the area containing 95% of bootstrap values (out of 10,000). (B) Note that when pooling all data together (from A panels) most species over-represented in the seed rain are rare species, while most cases of under-representation are from abundant species. (C) A multinomial logistic model confirms that seed dispersal shows negative frequency dependence as it can correctly classify dispersal categories (higher than expected [green], random [black], or lower than expected [magenta]) for all 25 species based just on relative seed availability of species (whole model test, preference category \sim proportion of abundance (month^{-1}) + plant species, $\chi^2 = 241.1$, $df = 25$, $P < 0.0001$, $r^2 = 0.53$; effect tests, plant species, $\chi^2 = 143.6$, $df = 24$, $P < 0.0001$; proportion of seed abundance, $\chi^2 = 56.6$, $df = 1$, $P < 0.0001$).

(Fig. 4A). Species producing fruits at much lower relative abundance in the community such as *Cordia polycephala* (CORPOL), *D. caribaeus* (DENCAR), and *Trichilia hirta* (TRIHIR) were dispersed more than expected by chance almost every month that were available (Fig. 4A). Dispersal significantly less than random was detected in six plant species, all of which were dominant in the plant community. Considering all species, the probability of being dispersed less than random was 0.75 when seeds of a given species composed $\geq 25\%$ of the seed availability in the community, which increased to a probability of 0.95 at a relative abundance of 40% of the community (Fig. 4C). On the other hand, the majority of species analyzed (17 out of 25) experienced dispersal higher than expected at least in one month when composing abundances $\leq 0.2\%$ of the fruit community availability (Fig. 4C). Despite this general trend, some species were never dispersed more than expected by chance, such as the common *Bourreria* spp. (BOUSP) and the uncommon *Ardisia obovata* (ARDOBO).

Plant emergence and recruitment in plots

Twenty-seven ornithochorous plant species established in our experimental patches with perches (Fig. 3C), a figure that represents 67.5% of the known species detected in the seed rain, and 59% of the plant species for which we have measures of fruit and seed availability. Plots without birds, in contrast, contained significantly less vegetation and no woody species in the 2-yr period than patches with bird dispersal (Fig. 2C and D). Recruitment was positively correlated to the availability of seeds in the environment and to dispersal frequency by birds (Appendix S1: Fig. S7). Overall, the three shade treatments patches of soil patches (no shade, artificial shade, or shade by *S. campanulata*, Fig. 1 and Appendix S1: Fig. S3) under bird plots had similar levels of plant species richness, growth, and seedling numbers (Appendix S1: Fig. S8).

Despite a reduction in species richness of 32.5%, the diversity (Shannon's H') and evenness (Pielou's J) of the community of recruits was higher than both the

community represented in the availability and the seed rain seed (Fig. 3). We even found establishment for four of the rare species for which we lacked availability data (Fig. 3, open bars), including a species (*Pimenta racemosa*) so rare in the site that was not even detected in the seed rain and for which we know no individuals in the study area: birds knew the site better than we did.

Bird abundance, frugivory, and the seed rain

The composition of bird communities active in pastures and forests were markedly different as shown by census data and a nonmetric multidimensional scaling ordination of point counts in pastures and forests (Table 1, Appendix S1: Fig. S9). Predominantly frugivorous species (*Turdus*, *Patagioenas*, *Spindalis*, *Loxigilla*, *Euphonia*) were restricted to forest patches, while granivorous species (*Tiaris* spp.) were the most common in pastures (Table 1). The only fruit-eating species active in pastures were the omnivorous Northern Mockingbird (*M. polyglottos*) and the Grey Kingbird (*T. dominicensis*), which are well known for having mixed diets of fruit and insects (Smith and Jackson

2002, Farnsworth et al. 2011). These two species showed the highest frequency of crossing activity between forest patches and open habitats, accounting for >90% of all observed inter-habitat movements (Appendix S1: Fig. S10). Furthermore, in 649 frugivory records collected in the study landscape, these two common bird species were also the most frequently detected feeding on fruit from the wider variety of plant species (Fig. 5A).

Perching activity was also clearly dominated by the omnivorous Mockingbirds and Kingbirds (Table 1, Appendix S1: Table S2). From the 12 bird species that we recorded using the perches, Mockingbirds and Kingbird accounted for 83.4% of the perching time of birds from all species (total perching time = 2379 min). Both Mockingbirds and Kingbirds contributed more than 40% of the cumulative perching time (Table 1), and their perching activity was positively correlated with both the intensity and species richness of the seed rain in our plots (Fig. 5B and C). The rest of the bird species accounted for less than 9.3% of the perching activity, made sporadic use of less than one-half of the plots, and their activity lacked relationship with the seed rain (Tables 1 and Appendix S1: Table S2).

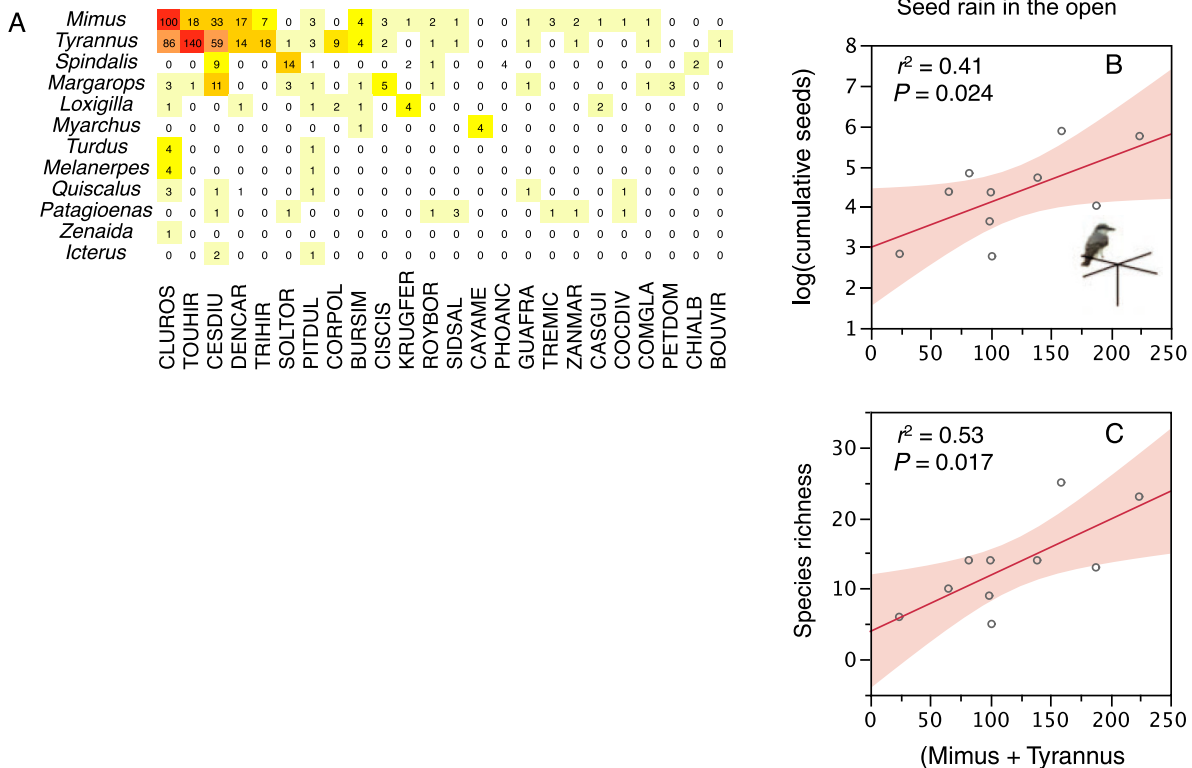


FIG. 5. Bipartite interaction network (A) showing the distribution of 649 frugivory records from 12 bird species among fleshy fruited plants at Finca Montaña in Aguadilla, Puerto Rico. Northern Mockingbirds (*Mimus polyglottos*) and Grey Kingbirds (*Tyrannus dominicensis*) dominated frugivory activity on the study landscape despite being omnivorous species. Observations were made by sampling activity systematically in forest patches, along edges, and in open areas throughout the site. Perching activity of Northern Mockingbirds and Grey Kingbirds was positively correlated with the (B) quantity and (C) richness of seeds arriving at seed traps under perches of the 10 experimental plots. Plant acronyms are explained in the caption of Fig. 3.

DISCUSSION

Our results show that bird frugivory can have strong equalizing effects on the dispersal of plant species in a community with vast interspecific differences in the relative abundance of fruit resources. Plant species differing in availability by three or more orders of magnitude showed similar, sometimes greater, quantities of dispersed seeds than common species with super-abundant crops. Diversity and evenness increased in the community of dispersed seeds and emerging plants as compared to the available seeds within fruit crops in the environment, demonstrating how an avian frugivory network can affect the reproductive potential of plants in a way that favors species of lesser abundance. Thus, our results suggest that rare-biased seed dispersal by frugivorous animals is an important mechanism structuring the diversity of recovering forests.

Frugivory and the initiation of forest succession

Bird dispersal not only increased the diversity of the seed rain and recruitment templates, it also triggered woody plant succession. Two years into the experiment, plant growth in plots with bird dispersal, which were dominated by seedlings and saplings of trees as well as fleshy-fruited shrubs, was over an order of magnitude greater than that of plots from which we excluded birds (Fig. 2C). Compared to plots with birds, plots without birds were in an early successional stage dominated by grasses and herbs (Fig. 2D). Thus, our results add to the mounting evidence that frugivory and seed dispersal mutualisms are key processes influencing the capacity of forest communities to quickly recover from major disturbances such as the deforestation-regeneration dynamics that are pervasive on tropical landscape (Guevara et al. 1986, Wunderle 1997, Chazdon 2014, Reid et al. 2015).

Two years into the experiment, plots with bird perches turned into small diverse nuclei of regenerating forest (Fig. 1 and Appendix S1: Fig. S3). Far from being an artifact of unnatural perches, we believe that this experiment has captured the general features of a widespread process. Regeneration on cleared tropical lands is patchy and depends on the formation of vegetation clusters or nuclei of vegetation that facilitate the establishment and expansion of woody plant cover (i.e., nucleation, reviewed by Corbin and Holl 2012). In turn, nucleation depends on the presence of a variety of perching structures and bird attractants such as fence lines, scattered shrubs and trees, stumps, fruit resources, etc. (Guevara et al. 1986, Holl 1998, 2002, Pizo and dos Santos 2011, Laske and Keitt 2012).

The quick development of diverse forest nuclei under perches may have been influenced by our control of seed predation (ant and rodent exclosures) during the first nine months of the experiment. Post-dispersal seed predation and density-dependent seedling mortality can be very high under bird perching sites receiving a copious

seed rain (Holl 1998, Spiegel and Nathan 2011, Carlo and Tewksbury 2014) and it can slow down plant establishment (Reid and Holl 2013). In fact, many of the bird-dispersed species we studied have been shown to suffer high predation rates under perching sites in open pastures (Carlo et al. 2013). Still, we were able to obtain the same levels of recruitment, diversity, and community composition in a follow-up experiment (2012–2015) in the site using new experimental patches where no seed predators were excluded (T. A. Carlo, *unpublished data*). Thus, we are confident that the rates of regeneration we observed in this experiment are similar to those under natural conditions.

In areas without perching structures or food resources to attract seed dispersal agents, tree species dispersed by wind can provide the initial perching structures that trigger or enhance nucleation. In Puerto Rico, wind-dispersed pioneers such as *Spathodea acampanulata*, currently the most abundant tree in Puerto Rico, have been shown to facilitate secondary succession in abandoned agricultural lands (Lugo 2004). In fact, it was common to see Kingbirds and Mockingbirds perching on saplings and small trees of *S. campanulata* towering above the grass. Furthermore, *S. campanulata* does not appear to interfere with early plant establishment in any significant way (Appendix S1: Fig. S8). Thus, our findings help to explain why successional forests in Puerto Rico and in other Neotropical locations in the mainland gain species quickly (Lugo 2004, Letcher and Chazdon 2009, Reid et al. 2015), highlighting the large influence of dispersal-assembly in the structuring and diversity maintenance of tropical forests (Terborgh et al. 2011).

Frugivory and seed dispersal in relation to seed availability

At first glance, rare-biased seed dispersal may seem contradictory to decades of research showing that frugivory is largely a positive density-dependent process. It is well documented that frugivores respond positively to the crop sizes of individual plants and neighborhoods (Davidar and Morton 1986, Saracco et al. 2005, Morales et al. 2012) and that they track fruit abundance across temporal and spatial scales (Levey 1988, Rey 1995, Saracco et al. 2004, García et al. 2011). Our results conform to these general patterns since the average availability of resources per species is positively related with the average number of seeds in the seed rain. However, this is far from being a one-to-one relationship and has a shallow positive slope (Appendix S1: Fig. S7). The shallow slope is due to the inclusion of rare species in frugivore diets, which implies that frugivores use fruit resources more evenly than expected by chance, reducing the dominance of the most common species in the seed rain (Fig. 2). For example, the six most common fruiting tree species had average densities of 10–100 seeds·m⁻²·month⁻¹, accounting for 91.3% of the seeds per fruit available for dispersal on the landscape (black bars,

Fig. 3A; note the logarithmic scale). Yet, seeds from these dominant species composed only 18.4% of the seed rain in our plots, whereas 43 plant species of lesser abundance accounted for the remaining 81.6%. Even several species for which we did not find any adult plants in our vegetation surveys were represented in the seed rain and recruitment stages (open bars in Fig. 2), showing that rare-biased dispersal could have strong influences on community assembly.

In addition to these community-level patterns, we found similar trends within species over time as their fruits seasonally changed in relative abundance. Four of the six most common tree species were over-represented in the seed rain when their fruits were seasonally rare, but under-represented when abundant (top panels, Fig. 4A). Even seeds of some rare species are likely to be underrepresented in the seed rain in months of peak abundance (mid and bottom panels, Fig. 4A), showing that antiapostatic selection can occur in both common and rare species.

Despite this general pattern in the seed rain, clear differences exist among species, reflecting a hierarchy of bird fruit preferences (sensu Carlo et al. 2003). For example, the factor “plant species” had a significant effect on our logistic model that classified species according to its level of dispersal (less than random, random, more than random, Fig. 3C). This suggests that the strength of antiapostatic selection among species is variable, and that the effect is stronger (i.e., penalizes a species more for having too much fruit) for less preferred species than for favorite ones. Evidence for hierarchical preference can be found in that some rare species (i.e., *Dendropemon caribaeus*, *Cordia polycephala*, *Trichilia hirta*; Fig. 3A) had many more instances (months) of higher-than-random seed dispersal than other rare species (i.e., *Cestrum laurifolium*, *Guettarda scabra*, *Ocotea coriacea*, Fig. 3A).

Alternative explanations to rare-biased dispersal such as the temporal partitioning of seed dispersal events between common and rare species are inconsistent with our data. This is because seeds of the majority of rare plant species appear co-dispersed in the late summer and fall months hand-in-hand with the seeds of the most abundant plant species during months of peak fruit abundance and diversity in the community (Appendix S1: Fig. S11). This rejects temporal partitioning as an important process determining frugivory and seed dispersal in this community since most rare dispersal events took place at times when competition for limited dispersal agents would be stronger. In turn, it is apparent that frugivores display tendencies to feed on multiple fruiting species over short time frames. Our data show that, for most plant species, just having ripe fruits available is a large determinant of chances of frugivory and seed dispersal (Figs. 2 and 3). This tendency to use more fruiting species than expected by chance implies that the functional responses of birds to the availability of a particular fruiting species are saturated (Holling type

II and III responses), and that saturate at lower values as there are more co-fruiting plant species. Hierarchical fruit choices of birds (preferences) could then explain community-wide variability in the slope and saturation point (asymptotic level) of species’ functional responses in a given fruiting scenario. In any case, it is clear that frugivore functional responses and preferences should be studied in more detail in order to get a better understanding of their role in the structuring and dynamics of plant communities via seed dispersal.

Why birds ingest and disperse the seeds of a wider variety of fruiting species when most of the time there are a few species bearing more fruit that can be possibly consumed? At least three non-mutually exclusive hypotheses may explain the use of rare fruit. Most fruits are typically low in nutrients and energetic rewards (Moermond and Denslow 1985), and consuming multiple fruiting species could serve to balance nutrients and energy (Whelan et al. 1998). Thus, fruits that provide complementary resources would promote dispersal of more species by placing upper bounds to the intake of abundant species, and extending frugivory and seed dispersal to less abundant species in the community. Similarly, secondary metabolites that protect fruits from microbes and herbivores could limit fruit intake, creating “attraction–repulsion” patterns that could diversify diets (Cipollini and Levey 1997). It is also possible that birds just try rare fruits out of sheer curiosity while scouting their territories. In fact, wild birds, particularly young and naïve individuals, readily try mimetic (Galetti 2002) or artificial fruits even if they have no previous experience with them (Weale et al. 2000). In any case, our results indicate that behavioral and physiological mechanisms underlying avian diet selection have direct consequences for the regeneration and species diversity of tropical forests.

Rare-biased dispersal and plant community diversity maintenance

The fact that many plant species in the community are over-represented in the seed rain when their seeds are relatively rare in the landscape can have far-reaching consequences for the maintenance of diversity and the coexistence of competing species. Theory and empirical evidence suggest that equalizing and stabilizing mechanisms involving different types of frequency and negative density-dependent processes are key for the maintenance of plant diversity (Chesson 2000, Muller–Landau 2008, Terborgh 2012). These types of processes are often collectively referred to as “advantage of the rare” (Terborgh 2012) that reduce mortality rates by pathogens, seed predators, herbivores, and lower intraspecific competition for resources (Janzen 1970, Uriarte et al. 2004, Comita et al. 2010). Still, the idea that interactions between seed dispersal agents and plants can also provide “rare species advantages” has not been entertained until now.

Our study suggests that rare-biased frugivory and seed dispersal is an overlooked process relevant to plant species coexistence and diversity maintenance. This is far from trivial when considering that dispersed and gut-treated seeds are almost invariably the ones that matter demographically (Traveset et al. 2007, Terborgh et al. 2011, Fricke et al. 2013). In light of the fact that the per-capita success of dispersed seeds is much higher than that of undispersed seeds (Swamy and Terborgh 2010), rare-biased dispersal can greatly reduce the effects of limited fecundity. Thus, relatively low rates of dispersal may be sufficient to insure that rare species remain represented in forest regeneration templates. Similar conclusions are reached by Terborgh et al. (2011) in a six-year study of the seed rain of a lowland Amazonian forest as they show that most trees are more strongly limited by fecundity (availability) than by dispersal. It is plausible therefore to consider rare-biased dispersal as an important stabilizing force in plant communities where frugivore-dispersed species are prevalent.

It is notable that two abundant generalist bird species, the Northern Mockingbird and the Grey Kingbird, were the main vectors of seeds into cleared areas and were responsible for the biases that resulted in increased plant diversity. Moreover, behavior and movements of these generalists connect two strikingly different habitats, which ultimately can benefit the rest of the frugivore community by spreading species important for the entire frugivore community into early successional forests. Species with similar foraging and movement habits (e.g., other tyrant Flycatchers and Mimidae, Thrushes, Bulbuls, etc.) that thrive in fragmented landscapes are likely to have similar effects on the seed rain in deforested lands elsewhere. But it remains as an open question whether rare-biased seed dispersal is a universal feature of plant–frugivore systems, or a trademark of certain omnivorous species such as Kingbirds and Mockingbirds.

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