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Birds as agents of seed dispersal in a human-dominated landscape in southern Costa Rica

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ABSTRACT

Birds play vital roles as seed dispersers helping to maintain and restore plant communities. With restoration increasingly key to global conservation, it is important to understand the landscape attributes and bird community characteristics that most influence avian seed dispersal in human-altered landscapes. We examined bird community structure and seed-dispersal patterns in agricultural countryside in Costa Rica that is typical of much of the Neotropics. Contrary to expectations, bird abundance, not richness, best predicted the richness of bird-dispersed seeds. Neither forest patch size or proximity, nor total tree cover, influenced seed dispersal. The richness and abundance of dispersed seeds, however, was strongly correlated with “wetness,” a remotely-sensed metric of vegetation, at several scales. These results suggest that in this human-dominated tropical region: (1) bird abundance, not species richness or size, may drive seed dispersal, and (2) remote-sensing combined with field verification can detect landscape elements that are helpful for maintaining the option of bird-mediated reforestation.

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1. Introduction

Many frugivorous birds are persisting, at least in the short-term, in human-dominated landscapes (Greenberg et al., 1997; Hughes et al., 2002), and these birds may serve important functions such as seed dispersal and pollination (Seker-cioglu, 2006). In their role as dispersers, birds are not only fundamental to the maintenance of diverse plant communities (Stiles, 1985), but may also have the capacity to restore them (Wunderle, 1997), thus potentially serving as important partners in tropical reforestation (Holl et al., 2000). However, despite numerous studies of frugivory and seed dispersal

(Howe and Smallwood, 1982; Willson, 1992), the consequences of frugivore diversity for seed dispersal in post-agricultural lands and the implications for forest regeneration remain poorly understood. Attention to this topic is critical given that opportunities for large-scale restoration now exist (Chomitz et al., 1999) and that birds may be one key to hastening the return of tropical forests which sustain biodiversity and supply ecosystem services for human well-being.

Our research integrates two major fields of inquiry: the study of bird assemblages in tropical landscapes (Martinez-Morales, 2005; Harvey et al., 2006; Borges, 2007) and the relationship between natural seed dispersal and forest

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regeneration (Da Silva et al., 1996; Holl et al., 2000; Au et al., 2006; Duncan, 2006). Even in intact tropical forests, seed dispersal can limit recolonization of forest gaps by pioneer species and regulate species richness (Hubbell et al., 1999). The conversion of forest to agriculture usually depletes the seed bank over time (Holl, 1999; Dosch et al., 2007), making natural succession reliant upon wind or animal-dispersed seeds which rarely travel far from intact forest (Nepstad et al., 1996; Duncan and Chapman, 1999; de Melo et al., 2006). Many studies, however, have shown that isolated trees or living fences, which are common in the humid tropics of Central America (Guevara et al., 1986; Slocum and Horvitz, 2000), can increase seed rain by serving as bird perches (Vieira et al., 1994; Shiels and Walker, 2003) and enhance seedling establishment with favorable microclimatic conditions (Uhl et al., 1982; Manning et al., 2006; Zahawi and Augspurger, 2006). Although we do not expect reforestation to occur on lands managed for agriculture, when cattle are excluded and other management practices halted, the combination of frugivorous birds and remnant trees can lead to the rapid recolonization of forest species (Janzen, 1988; Guevara et al., 2004). Determining what characteristics of the bird community in actively managed lands could contribute to forest recovery is crucial because management strategies to increase rates of seed dispersal are more likely to be successful, and perhaps more cost-effective, if they rely on natural processes (Duncan and Chapman, 1999). Our study addresses aspects of bird communities, and the vegetation they depend upon, that could preserve options for the future if and when land is taken out of production with the goal of reforestation.

The relative importance of characteristics of the bird community – richness, abundance and mean body size – on seed dispersal in human-dominated landscapes may depend on whether countryside frugivores tend to be generalist or specialist fruit-feeders (Howe, 1993; Saracco et al., 2004). Under the first scenario, species may persist in agricultural areas because their generalist diet allows them to adapt to new habitats; i.e. when important food sources disappeared in the conversion from forest to agricultural, the birds that survived were capable of readily switching sources. Alternatively, avian frugivores in countryside habitats may persist precisely because they specialize on the fruit of common plants that thrive in these areas (Kissling et al., 2007). Whether the birds that persist in human-dominated areas are largely generalist or specialist seed-dispersers has important implications for species extinctions (if specialists are lost), plant invasions (Renne et al., 2002) and patterns of seed distribution and regeneration (Howe, 1993).

The spatial and temporal scales at which birds interact with fruiting plants is also likely to influence the quantity and richness of seeds dispersed. If birds make minimal movements between consuming and defecating seeds, then patterns of seed dispersal would be driven largely by local phenomena, i.e. the richness and abundance of fruiting trees in the immediate vicinity of where the seeds are dispersed. In contrast, if birds are drawing on food resources over a larger scale during a digestive cycle, then landscape-level vegetation cover may be more important than the local plant community. Thus, depending on how birds use resources, three types of measurable plant cover might be correlated with seed dis-

persal variables. If birds are heavily dependent on remnant forest, then the size of these forest patches and their proximity to seed dispersal sites could strongly influence the nature of seed dispersal. If, however, vegetation throughout the landscape (e.g., secondary forests, living fences, scattered trees, and gardens) matters as much or more to bird persistence and movement, then a measure of all tree cover should correlate well with seed dispersal variables. Finally, if herbaceous plant growth is also a key factor to birds (e.g., providing cover for small-bodied birds or for harboring arthropods to supplement fruit in the diet) in combination with tree/shrub cover, then a remotely-sensed metric of this vegetation, such as wetness, might best correlate with patterns of seed dispersal and be the best means of determining the scale over which frugivorous birds use resources.

Here we report on important factors predicting patterns of seed dispersal in a human-dominated landscape in southern Costa Rica. We hypothesized that the richness and abundance of seeds dispersed will be positively correlated with the following characteristics of the bird and plant community: (1) bird richness, abundance, and body size; (2) local vegetation cover (tree richness and abundance); and (3) regional vegetation cover (remnant forest area, proximity to forest, and tree cover). Although we expect that all of these variables will be positively correlated with seed dispersal, we predict that some variables will be more important than others due to factors such as the degree of bird specialization on fruit resources, the distribution of these resources, and the spatio-temporal scale of bird foraging. We tested our predictions by surveying birds and bird-dispersed seeds at six sites in the Costa Rican countryside and then assessing vegetation richness, abundance, distribution and productivity at several scales around each site.

2. Materials and methods

2.1. Study area

We studied patterns of seed dispersal in the human-dominated landscape of the Coto Brus region of southern Costa Rica (Fig. 1). This area ranges in elevation from 750 to 1250 m, has a mean annual rainfall of 3420 mm and occurs largely in the ‘tropical premontane rainforest’ Holdridge Life Zone (Tosi, 1969). Approximately 80% of this region was deforested in the 1950s and 1960s (Sanchez-Azofeifa, 1996). As a result, the landscape is now a mosaic of small forest fragments (<10 ha) and sparsely shaded coffee, cattle pasture and human settlements (Daily et al., 2001). About 25% of the area remains forested, 23% is in pasture, 15% is cultivated for coffee, and the remaining land is occupied by small towns and a variety of fruit trees and vegetable crops (Ranganathan et al., 2007). Pastures, coffee plantations and other cropland contain scattered isolated trees that do not form a continuous canopy and are often bordered by live fences. The population density is 47 per sq km in the Coto Brus region and some deforestation and agricultural intensification (e.g. rustic coffee to technified plantations with no trees; and coffee to pineapple or pasture) continues (Lindell et al., 2004). For more detailed descriptions of the study area please refer to previous publications (Daily et al., 2001; Ricketts et al., 2001; Hughes et al.,

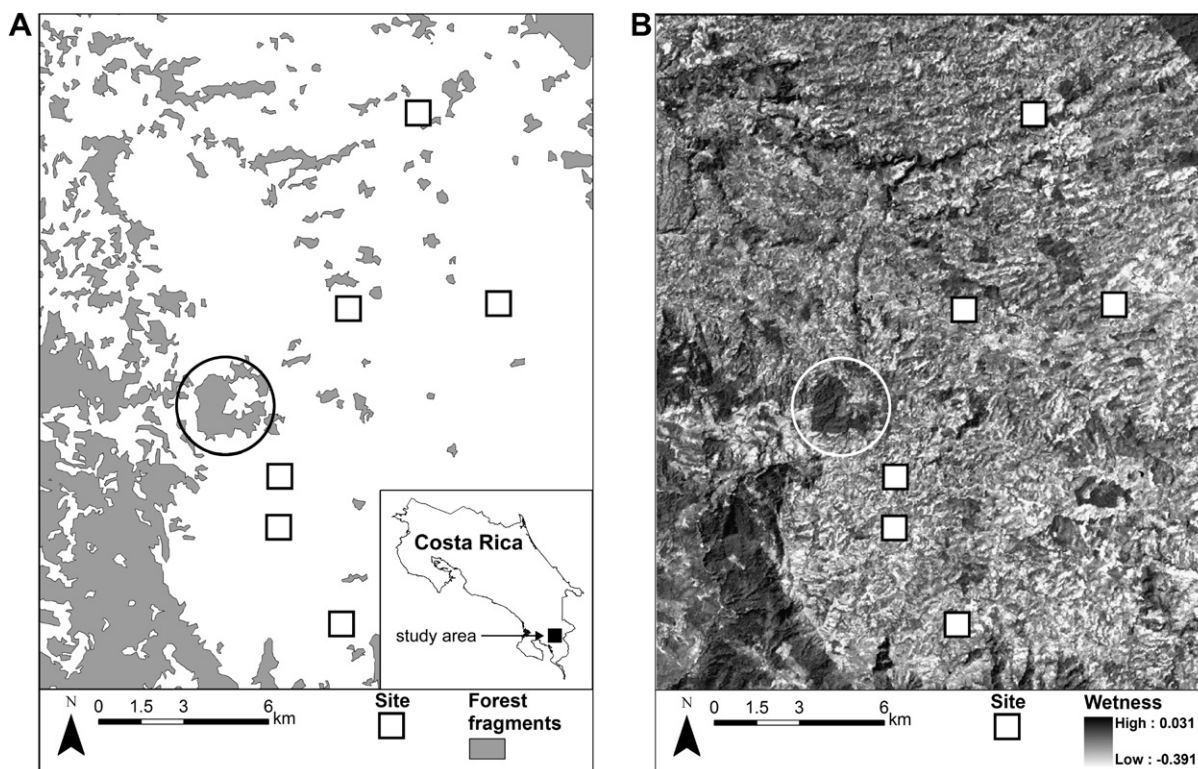


Fig. 1 – The six survey transects (white boxes) are overlaid on two contrasting images of the study site in the Coto Brus region of southern Costa Rica. (A) A map of remnant forest (gray), and human-dominated lands (white) (Daily et al., 2001). (B) A map of wetness in the same region (darker areas = more vegetation cover). The Las Cruces forest and biological station is circled on both images. The figures were derived from a 21 January 2003 Landsat 7 ETM+ image.

2002; Sekercioglu et al., 2002; Daily et al., 2003; Luck and Daily, 2003; Mayfield and Daily, 2005; Brosi, 2007; Ranganathan et al., 2007; Sekercioglu et al., 2007).

Survey sites. We surveyed six sites within 15 km of the Las Cruces Reserve, one of the larger remnants of native forest embedded in this agricultural area (227 ha) (Fig. 1). All bird, seed, and tree sampling at each site took place within a 200 m × 100 m plot centered around a 200-m transect. Transect length was based on a desire to efficiently sample sites across a broad spatial scale. Our goal was to cover a range of independent sites and to survey each site well before it got too warm and bird activity decreased. We chose 200-m transects so that we could sample all sites multiple times. The surveys were done as transects rather than area searches because of the problems associated with crossing roadside fences and entering private property.

Each transect ran through some combination of pasture, coffee, remnant vegetation, living fences and small fruit and vegetable plots. The vegetation cover at two sites was dominated by sun coffee with scattered trees and shrubs. Cover at two additional sites was predominately small coffee, fruit and vegetable plots near homes and bordered by living fences. The remaining two sites were a mix of cattle pasture, living fences, coffee and fruit trees. These sites were non-randomly selected to fall out along a gradient that is broadly representative of the heterogeneous human-dominated landscape in this region of the neotropics.

2.2. Bird surveys

The six sites were surveyed in 2005 and 2006 by J.R. Zook, an ornithologist specializing in Costa Rican avifauna. These bird surveys are part of a long-term country-wide effort to document bird assemblages in human-dominated landscapes in Costa Rica. We have been collecting this information biannually (three surveys per season per site per year) at these six transects, and 42 others in four regions of the country, since 2000 (G.C. Daily, unpub. data). We used only the bird survey data from 2005 and 2006 because these surveys took place immediately before and after our seed-dispersal assays and thus they are most likely to reflect the relevant assemblage of birds. We suggest that this level of sampling is sufficient given that the 2005–2006 surveys captured 76.8% of the total species pool of frugivorous birds observed at our six sites over the full seven years of surveys (2000–2006).

Each of the six 200-m transects were walked between 0530 and 0900 on three different days during February–April of both years. Of the 36 total surveys, 18 occurred in February, 12 in March and six in April. Each survey lasted 30 min, and all birds heard or seen within 50 m lateral distance of each side of the transect were recorded. We calculated the mean relative abundance and observed richness per site for frugivores only. We used body mass data from Stiles and Skutch (1989) weighted by the number of individuals of each species to calculate the mean body mass of the frugivorous bird com-

munity at each site. We classified species as frugivorous (feeding either partly or entirely on fruit) based on information in Stiles and Skutch (1989) and personal observations. Although we were only able to collect seed data in 2006, there were no major changes in vegetation between the two years at any of the sites.

We used EstimateS (Colwell, 2006) to calculate non-parametric estimators of total species richness. We report the first-order Jackknife estimator (Chao, 2005) because it has performed well in previous investigations of benchmark datasets (Magurran, 2004).

We do not attempt to estimate bird densities using distance-sampling approaches because in these species-rich avian communities there were too few detections of most species to yield reliable estimates (recommended $n > 75$ –100; Buckland et al., 2001; Somershoe et al., 2006). Moreover, recent reviews strongly discourage the lumping of species to compare communities using programs such as DISTANCE (Rosenstock et al., 2002; Thomas et al., 2005). Therefore, we have instead attempted to reduce observer- and visibility-bias by using a single expert observer in relatively open countryside and by standardizing transect and survey length (Dieffenbach et al., 2003).

2.3. Bird-dispersed seeds

Using seed traps, we collected bird-dispersed seeds from each site three times in February–March 2006. Seed traps were composed of round coffee baskets covered with fine mosquito mesh forming an inner bowl and affixed to each basket with clothes pins. The surface area of each trap was 1250 cm². Seed traps were in place by 05:30 (shortly after dawn) when bats, which forage nocturnally, are no longer active (Medellin and Gaona, 1999; Galindo-Gonzalez et al., 2000). Seeds were collected and traps removed at 09:00, corresponding to the end of the bird surveys and a dramatic drop in bird activity.

Each sampling morning, we placed 100 seed traps in groups of five under 20 trees or tight groups of trees spaced relatively evenly along and within 10 m of the 200 m bird transect. We used the following protocol to select where to place the traps. First, we divided the 200 m transects into four 50 m sections. In each section we chose a random number between zero and four to determine where to begin placing the traps (0, 10, 20, or 30 m). Second, we placed the traps in groups of five under five randomly selected trees or groups of trees within the following 20 m stretch of the transect. Thus, the traps were laid out in four relatively evenly distributed sections along each transect but the exact location of the seed traps within each section was random.

Because our study sites were embedded in an agricultural landscape where people live and work, we monitored our seed traps throughout the entire period they were open to ensure that they were not compromised by cows, dogs, children, or farm operations. Because we were operating seed traps in this environment and with these constraints, we could only open seed traps at one site/morning.

At the end of the sampling morning, all tree and shrub seeds found on the surface of the cloth in the form of bird feces were placed in glass vials with 80% ethanol. Care was taken to only collect seeds dispersed by birds (i.e., no seeds still

enclosed by fruit and obviously undamaged, and no grass seeds). We then used a light microscope to sort all seeds from each sampling morning into morphospecies. We described and attributed a code to each morphospecies, recorded the number of each type, and used electronic calipers to measure the length and width of one seed from each morphospecies per day. The morphospecies were later identified taxonomically to family or genus, when possible, using reference collections compiled by previous investigators (Werner, 2004).

2.4. Vegetation cover

To determine how local and landscape-scale vegetation influences bird and seed richness and abundance, we used different methods to measure three types of plant cover that span 10 m, 100 m, 500 m and 1000 m zones or “buffers” around each transect. The plant cover types were: (1) local (10 m) tree cover (from field surveys), (2) regional (100 m, 500 m, 1000 m) forest cover and proximity (from an existing GIS layer; Daily et al., 2001), and (3) regional (100 m, 500 m, 1000 m) wetness, a remotely-sensed metric of vegetation cover (from a transformation of Landsat data) (Fig. 1). We chose the buffer areas based on a priori ecological knowledge: (a) 10 m is an appropriate minimum buffer distance because it is approximately the scale of influence of individual trees, and (b) a previous study in our study region used radio-transmitters to track three frugivorous bird species (21–72 g) in the same human-dominated habitat and found that 97% of daily movements were within a 500 m radius (Sekercioglu et al., 2007). We collected vegetation data wherever possible for 100 m and 1000 m buffers around each transect as brackets around the 500 m benchmark.

Local tree cover. We recorded tree abundance and tree species richness adjacent to each transect. We counted and identified all trees and shrubs >3-m tall within 10 m of each 200-m transect (over the same area in which seed traps were placed). For each tree, we recorded the species name, distance from transect, and whether the tree was fruiting or flowering.

Total forest area and proximity. Because the richness and abundance of birds and the seeds they disperse may be influenced by remaining forest in the landscape, we determined the distance from each transect to the nearest small (0.1–100 ha), and large (>100 ha) forested area (Daily et al., 2001) (Fig. 1). We also recorded the number of forested areas within 100 m, 500 m and 1000 m of the transect, and calculated the total area of forest cover within these buffers.

Wetness. This remote sensing metric is derived from a tasseled-cap transformation (also known as a Kauth–Thomas transformation) of a Landsat ETM+ image (Crist and Kauth, 1986). Wetness has been strongly correlated with land use and vegetation cover in our study region (Ranganathan et al., 2007) and elsewhere (Helmer et al., 2000; Aguilar, 2005). This metric is easily calculated and biologically meaningful because it is a reflection of soil and canopy moisture (Cohen and Goward, 2004). We selected wetness over the Normalized Difference Vegetation Index (NDVI) because NDVI is known to saturate in the tropics (Kerr and Ostrovsky, 2003).

We used a Landsat ETM+ image of the Coto Brus study area captured on January 21, 2003, the most recent cloud-free image without data gaps to explore correlations between wet-

ness and patterns of seed dispersal (Fig. 1). We chose a dry-season image to correspond with the season of our sampling and calculated mean wetness at three scales: 100 m, 500 m and 1000 m buffers around each transect. The sample variogram for the gridded wetness data of the study region showed that the sill was reached at a range of 300 m, indicating that there is no spatial autocorrelation for wetness-seed associations between 100 m, 500 m and 1000 m buffer radii.

2.5. Statistical analyses

We employed a likelihood approach to determine the relative importance of each bird community variable in influencing seed richness and abundance (Burnham and Anderson, 2002). We used this approach because it allows a direct comparison of the strength of potential correlations between bird or habitat variables and patterns of seed dispersal. This technique is appropriate here because our goal is less to test for significance than to determine how these variables rank in importance. Determining the relative role of various habitat and bird community variables provides insights into the key components of agricultural systems that should be maintained in reserve for future forest restoration efforts.

We built two sets of candidate models to determine how three characteristics of the frugivorous bird community – richness, abundance and size of individuals – contributed to the variation in the diversity and abundance of seeds dispersed. The predictor variables for the first set of models (seed richness) were bird richness, body-mass range, and bird abundance; those for the second set of models (seed abundance) were bird abundance, mean body mass, and bird richness. We include body size (mean and range of mass) as a predictor variable because we would expect a community composed of larger birds to ingest more seeds, and a community composed of a greater variety of bird sizes to ingest a greater variety of seeds, thus influencing the abundance and the richness of seeds dispersed, respectively. Strong collinearity was not detected among the predictor variables (variance inflation factor < 2.86 for all pairs of variables).

We used the second-order Akaike Information Criterion (AIC_c), which is adjusted for small sample sizes (Burnham and Anderson, 2002), to evaluate support for both sets of models. By subtracting the minimum AIC_c value of each set of models from each model in the set, we obtained Δ_i values (models with $\Delta_i \leq 4$ have strong empirical support: Burnham and Anderson, 2002). We used the Δ_i values to calculate Akaike weights (w_i), which reflect the likelihood that a given model is the best in the candidate set, and which allowed us to rank the contribution of each variable to the richness and abundance of seeds dispersed (Burnham and Anderson, 2002).

We were unable to use the likelihood approach to assess the importance of the vegetation variables on seed dispersal because we chose to analyze these data at multiple scales, resulting in too many predictor variables relative to our sample size. Thus, we used linear regression and the nonparametric Spearman's rank correlation coefficient to test for correlations between seed richness and seed abundance and the three types of plant cover (see Section 2.4).

3. Results

We recorded 119 bird species at our sites (sampling effort: 540 min/yr), of which 72 (60%) were at least partially frugivorous (Stiles and Skutch, 1989; personal observations). We documented 65 tree species growing immediately alongside the transects, of which 37 species (57%) produce fruit consumed by birds. Tree density varied from 112.5 to 335 trees/ha. Overall, we collected 46 species of bird-dispersed seeds in our traps during 63 h of sampling. Twenty-five of these species were identified at least to genus. None of the identified seeds came from species restricted to forest, and only nine identified seeds came from tree species found along the transects.

3.1. Effects of the bird community on seed dispersal

The linear model with frugivore abundance alone strongly accounted for patterns in seed richness in this human-dominated landscape ($w_i = 0.98$; $r^2 = 0.95$; Table 1). This model was more than 20 times more likely than any other model in the set to predict the richness of seeds dispersed; all other models had essentially zero empirical support. In the set of models for seed abundance, the two models containing the single variables frugivore abundance and frugivore richness, were both strongly supported (abundance $w_i = 0.40$, $r^2 = 0.71$; richness $w_i = 0.47$, $r^2 = 0.73$) (Table 1). Although bird mass range was not important for seed richness ($w_i < 0.01$, $r^2 = 0.32$), mean bird mass was somewhat important for seed abundance ($w_i = 0.09$, $r^2 = 0.53$) (Table 2). The models with multiple variables explained very little about the richness and abundance of seeds dispersed.

3.2. Effects of vegetation cover on seed dispersal

Of the three indices of vegetation cover, only wetness was significantly correlated with the richness and abundance of seeds dispersed. At the local scale (10-m buffer around transect) there was no relationship between any type of tree abundance (all trees, potentially fruiting trees, and currently fruiting trees) and seed dispersal (all $P > 0.07$). Similarly, no measure of forest cover (total forest area within buffer or dis-

Table 1 – Model selection and goodness-of-fit results for bird-dispersed seed richness and seed abundance

Models	AIC_c	K	Δ_i	w_i	r^2
<i>Seed richness models</i>					
Frugivore abundance	13.79	2	0	0.98	0.95
<i>Seed abundance models</i>					
Frugivore richness	7.80	2	0	0.47	0.73
Frugivore abundance	8.14	2	0.34	0.40	0.71
Mean mass	11.05	2	3.25	0.09	0.53

In the analysis, each set of models included all possible combinations of three predictors or characteristics of the bird community (frugivore abundance, richness and body size). In the results, all of the models with strong levels of support ($\Delta_i \leq 4$) had just one predictor; only these are shown here. Akaike weights (w_i) express the relative likelihood of each model and the r^2 values demonstrate the strength of each relationship.

Table 2 – The relative importance and rank of each characteristic of the frugivorous bird community in predicting bird-dispersed seed richness and abundance

Frugivore variable	Importance	Rank
<i>Seed richness models</i>		
Abundance	0.99	1
Richness	0.01	2
Mass range	<0.01	3
<i>Seed abundance models</i>		
Richness	0.49	1
Abundance	0.44	2
Mean mass	0.12	3

The importance of each variable was calculated as the sum of all w_i from models containing variable x divided by the sum of all w_i (see Table 1 for w_i values).

tance to nearest forest patch) correlated with seed richness or abundance (all $P > 0.21$).

Although wetness also did not correlate with any measure of seed dispersal across all six sites (all $P > 0.25$), one site was a consistent outlier at every scale, probably due to the high percentage of exotic tree cover (*Pinus* sp.) documented during field surveys. Such non-native canopy trees increase wetness values which may lead to misleading results because *Pinus* provides poor habitat for bird communities (Petit et al., 1999; personal observations). In contrast, every other site was quite typical of tropical countryside: a mosaic of pasture, crops and woody vegetation with no unusual cover of non-native and/or non-fruiting trees.

Over the five remaining transects, although we found no significant correlations within the 100-m buffer (seed abun-

dance: $r^2 = 0.54$, $P = 0.16$; seed richness: $\rho = 0.70$, $P = 0.23$), wetness was strongly correlated with the richness and abundance of seeds dispersed at the larger spatial scales: 500-m buffer (seed abundance: $r^2 = 0.98$, $P = 0.002$; seed richness: $\rho = 0.1$, $P = 0.02$); 1000-m buffer (seed abundance: $r^2 = 0.99$, $P = 0.0005$; seed richness: $\rho = 0.90$, $P = 0.08$) (Fig. 2). At both 500 and 1000-m buffer distances, the strongest relationship between wetness and seed abundance was linear and the best fit between wetness and seed richness appears to be a positive saturating curve (Fig. 2).

4. Discussion

The number of individuals rather than the number of frugivorous bird species was the key factor driving seed dispersal in this study site in southern Costa Rica (Table 2). This result is consistent with a “generalist” bird community scenario: if fruit-eating birds in human-dominated landscapes feed broadly, we would expect frugivore abundance rather than richness to drive seed dispersal (Table 1). High bird species richness may therefore be less relevant than previously thought to ecological functions such as seed dispersal in human-dominated tropical landscapes (Fleming, 2005; Kissling et al., 2007). Maintaining high bird abundance, however, may be crucial to maximizing the role birds play in sustaining and enhancing forest cover in these areas into the future. Given that our results are from six transects in one agricultural landscape, studies investigating if this pattern is more broadly true would be of great utility.

We found that frugivorous birds disperse pioneer plants that might help pave the way for reforestation but are not representative of nearby rainforest. Although birds at our sites did disperse seeds from outside the immediate vicinity of

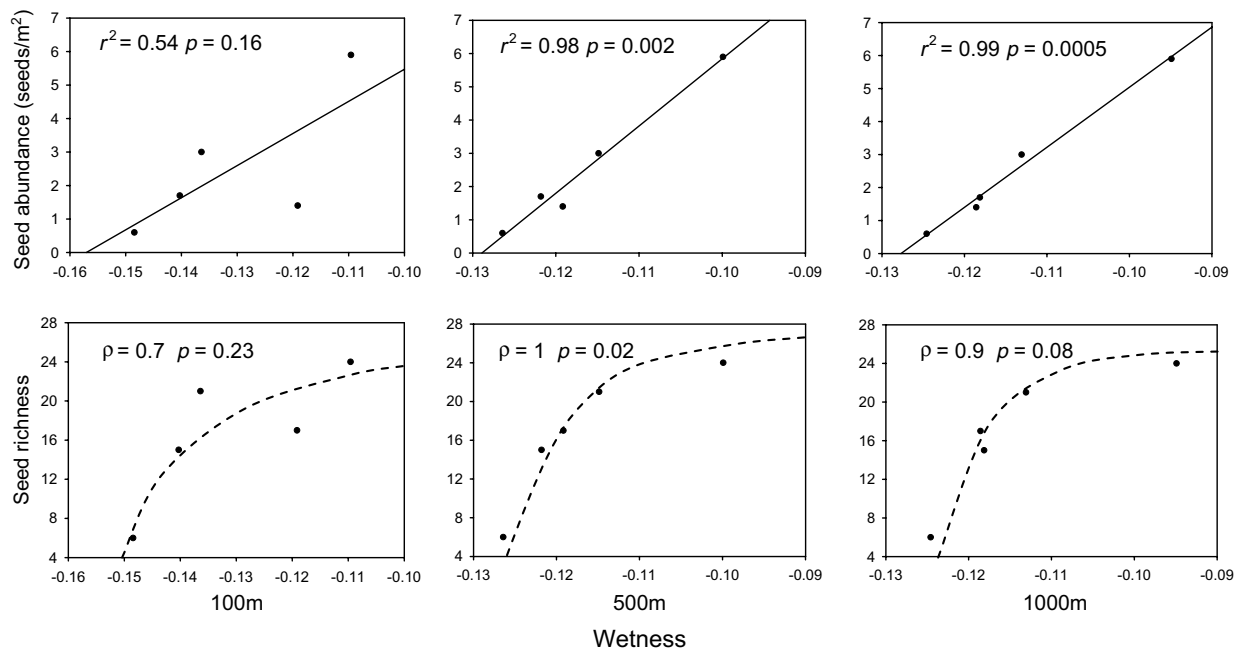


Fig. 2 – The relationship between bird-dispersed seeds (richness and abundance) and wetness at three spatial extents: 100-m, 500-m, and 1000-m buffers around each transect. The dotted lines indicate that the relationship between wetness and seed richness appears to be a positive saturating curve.

the transects, we did not detect frugivore-mediated seed dispersal of forest-restricted tree species into deforested habitats. The dominant species along our transects and in our seed traps were woody plants in the genera *Cecropia*, *Erythrina*, *Solanum*, *Croton*, *Piper*, and *Psidium*. Although this is a limited and skewed assemblage of species available for forest recovery, these species can provide shade and/or fix nitrogen (e.g. *Erythrina* and *Croton* spp.) thereby facilitating conditions for native forest species to establish (Nepstad et al., 1996; Montagnini, 2005; Neilan et al., 2006). Many of these species are potentially important pioneers that have been found in the seed bank of secondary forests (Young, 1985) or that have been proposed as suitable candidates to outplant as a first step towards reforestation (Holl et al., 2000). Because seed availability is a limiting factor to forest recovery in human-dominated lands in Costa Rica (Wijdeven and Kuzee, 2000), it is encouraging that at our sites birds are actively dispersing seeds of these pioneer plants. Depending on proximity to seed sources, previous land use (e.g. cattle grazing) and other landscape factors, achieving full rainforest recovery may require supplementing the services that birds provide with active planting of additional desirable species (Wijdeven and Kuzee, 2000).

Our vegetation cover analyses demonstrate that the elements of the landscape that are important for maintaining high bird abundance, and thus high seed dispersal, are subtle. Remotely sensed wetness was the only significant predictor of seed richness and seed abundance, apparently a far better single measure of the plant resources important for frugivorous birds than either forest remnants or local tree cover. Field measurements of regional woody vegetation cover may yield more accuracy, but would be a very time-intensive approach. Wetness, in contrast, is relatively quick to calculate (Ranganathan et al., 2007) and correlated surprisingly well with the richness and abundance of seeds dispersed (Fig. 2).

Wetness may have been the best measure of food resources for frugivores because it is a continuous rather than a categorical measurement (Defries et al., 1995) (Fig. 1). As a reflection of canopy moisture, wetness is a measure not only of remnant forest but also all of the other vegetation that may matter to birds in agricultural areas. Perennial vegetation in yards, gardens, pastures and crop fields, along roads and in living fences has been shown to be more productive and to support more diverse and abundant bird communities than closely cropped pasture (Harvey, 2000; Hughes et al., 2002). These patches of herbaceous and woody cover, reflected in higher wetness values, may increase the supply of invertebrate prey and provide cover for the small species that dominate the frugivorous bird community. Thus, our remote sensing results indicate that maintaining this sort of cover in a human-dominated landscape also maintains the frugivorous birds which, as vectors for seed dispersal, could be important contributors to the regeneration of abandoned land in the future (Luck and Daily, 2003).

We found that the scale of analysis matters in detecting those landscape elements relevant to seed dispersal. Bird mobility means that frugivores can select habitat over large landscape scales (Gaston, 2003). For instance, Garcia and Ortiz-Pulido (2004) showed that frugivore activity was positively correlated with fruit availability on the landscape scale, but not on the local scale. These results parallel those of our study;

seed dispersal was significantly correlated with wetness at larger scales (500–1000 m), but not correlated with vegetation characteristics at the local scale around each transect (Fig. 2). Importantly, our use of remotely-sensed wetness suggests that this tool can be applied in novel ways to indicate the spatial extent over which frugivorous birds interact with their landscape, thereby influencing ecological processes.

Several groups of potential seed dispersers are missing from this study such as frugivorous bats, monkeys and large frugivorous birds. Because data on bat richness or abundance for the Coto Brus region is limited, we chose to exclude bat-dispersed seeds from this study. Bats, however, may be filling a different but equally important niche as seed dispersers in human-dominated areas and thus deserve additional attention for their role in restoration (Galindo-Gonzalez et al., 2000; Evelyn and Stiles, 2003).

Large vertebrate species, both monkeys and birds, which disperse large-seeded canopy species are often the first to disappear from human-dominated areas (Wunderle, 1997). We found that this pattern held true for birds in our study area, and Daily et al. (2003) found large frugivorous mammals conspicuously absent from human-dominated lands in the same region. Dispersal by the many smaller bird species we detected, however, could catalyze the first phase in rainforest restoration. In time and in the ideal, larger bird species and other fruit-eating taxa may be attracted back to these areas (Luck and Daily, 2003).

This study was designed to determine the relationship between the frugivorous bird community and seed dispersal during the dry season only. We selected this season because the major plant families in this landscape produce seed in both seasons (Dosch et al., 2007), but the heavy rains that can occur in the wet season make it difficult to collect accurate data on seed rain. The dynamics between the bird community and the abundance and richness of seeds-dispersed may differ at other times of the year because the dry season bird community is uniquely characterized by an influx of in wintering migrants. The migrants in our study area, however, are largely insectivorous rather than frugivorous and were in the minority relative to the overall bird community (14% of species; 8% of individuals). Thus, although migrants may play a role, they are unlikely to have driven the patterns we report.

Nearly half of the bird species in our study region (Hughes et al., 2002) and more than 70% in other places (Estrada et al., 1997) are using human-dominated lands. It is not known whether these populations are stable, but it is likely that they are providing key functions including seed dispersal and pollination (Sekercioglu, 2006), and if sustained, could reduce the costs of restoration in the future (Hougnier et al., 2006). Naturally, the capacity of animals to contribute to restoration depends on the availability of both seed sources (Janzen, 1986) and seed dispersers (Wunderle, 1997). To reforest with the help of frugivores, it is imperative to protect and enhance key landscape elements, such as vegetation outside forested areas, at a scale that matters for birds. This study suggests that by using remote sensing in tandem with field studies of ecosystem processes, we can better understand both. Reforesting the tropics for biodiversity and human well-being will surely be far more efficient if we preserve the option of benefiting from the ecological services that birds provide.

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