**Resource tracking weakly links species richness in food resources, seed vectors, and seed rain**

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**ABSTRACT:**

1. Within the context of global change, seed dispersal research often focuses on changes in vector assemblages rather than vector behavior. Furthermore, many of those studies are conducted in a tropical biome with large-bodied frugivores that are sensitive to habitat fragmentation. In other parts of the world, vertebrate disperser assemblages may be more robust to fragmentation, but global change may still generate consequences for seed dispersal by influencing vector resource tracking.
2. We hypothesized that resource tracking may promote diffuse plant-animal dispersal mutualisms if resource richness is positively linked to vector and seed rain richness. We predicted that increasing resource richness attracts more visits and species of vertebrate vectors, resulting in higher counts and greater species richness of seed rain.
3. We experimentally tested this mechanism in two replicated field experiments using a model system with bird feeders positioned above seed traps. In the first experiment, we demonstrated that resources skew seed rain. In the second experiment, we explored how the species richness of food resources (0, 4, 8, or 12 different species) affected the species richness and visitation of avian vectors present at feeders and in subsequent seed rain. Collectively, we observed a positive relationship between available food resources and seed rain, likely mediated by the resource tracking behavior of avian vectors.
4. Our findings underscore a potential key mechanism that may facilitate diversity, whereby accumulating species richness in the plant community indirectly promotes more species in seed rain. Importantly, the resource tracking mechanism driving this potential positive feedback loop may also result in negative ecosystem effects if global change alters resource availability. Moving forward, future research should explore the bottom-up effects of global change on food resources and vector behavior to compliment the body of literature regarding changes in vector assemblages.

*Key words*: *avian seed* *dispersal, mutualism, diversity-maintenance mechanism, resource-tracking, zoochory*

**INTRODUCTION**

Global biodiversity is declining, in part, due to shifts in the availability, distribution, and quality of resources and habitat components that support ecological interactions (Jordano, 2016; Tylianakis et al*.*, 2008; Sala et al., 2000). Habitat loss and fragmentation continues to diminish the availability and quality of space, contributing to an asymmetric skew in the loss of biodiversity with the extinction of animals at higher trophic levels and smaller population sizes occurring first (Dirzo et al., 2014; Duffy, 2003; Estes et al., 2011). Such losses raise concerns globally regarding the top-down effects of decreasing biodiversity on the assembly and stability of ecosystems (Donoso et al., 2020; Powers & Jetz, 2019; Spooner et al., 2018; Wang & Loreau, 2016). However, the consequences of global changes may differ across regions and biomes (Bowler et al., 2020).

While seed dispersal mutualism research related to anthropogenic impacts is evenly distributed between temperate and tropical regions, nearly half of all studies occurs in the tropical and subtropical moist broadleaf forest biome (Teixido et al., 2022). Seed dispersal relationships are generally diffuse mutualisms, defined as a mutually positive relationship including multiple participating species (e.g., pollination, seed dispersal, and mycorrhizae; Gove et al., 2007; Stanton, 2003; Zamora, 2000). In tropical forest biomes, asymmetric declines in the large-bodied components of diffuse mutualisms with habitat fragmentation are hypothesized to diminish biodiversity, particularly when some plants are only dispersed by a subset of dispersers (Bovo et al., 2018; Case & Tarwater, 2020; Naniwadekar et al., 2019). More specifically, the loss of large-bodied frugivores from fragmented landscapes can limit dispersal distances and strengthens dispersal limitation, potentially resulting in negative impacts on larger-seeded plants (Cordeiro & Howe, 2002; Cramer et al., 2007; Jordano et al., 2007). Seed dispersal by bird assemblages in temperate region forest biomes may be more robust to habitat fragmentation than in tropical biomes (Bregman et al., 2014; Farwig et al., 2017; but see Fontúrbel et al*.*, 2015). However, most seed dispersal research related to anthropogenic impacts in temperate regions still focuses on fragmentation (Teixido et al., 2022). This discrepancy underscores the need to reevaluate seed dispersal processes for a more robust understanding of how global changes affect seed dispersal relationships.

Whereas much of the research on fragmentation stresses the top-down effects of species loss, changes to vector behavior associated with global change may also drive bottom-up effects on seed dispersal mutualisms. For example, introduced resources can disrupt or promote seed dispersal mutualisms (Gleditsch & Carlo, 2010; Rojas et al., 2019; Traveset & Richardson, 2006; Sengupta et al., 2015). Indeed, food resources play a particularly influential role in seed dispersal by linking frugivore and plant diversity (García & Ortiz-Pulido, 2004). The effect of food resources on seed dispersers is often studied using a resource tracking framework, which could be broadened to include other habitat components (Gleditsch et al., 2017; Mason et al., 2022). According to this perspective, perches (Holl, 2002; Verdu & Garcia-Fayos, 1996), cover (Alcántara, 2000; Herrera et al., 2011), and fruit (García et al., 2011; Gleditsch & Carlo, 2010; Rodríguez-Pérez et al., 2014; Saracco et al., 2004), can indirectly attract seed rain by concentrating behavior of many vectors (Gleditsch et al., 2017; Jongejans et al., 2015; Kwit et al., 2004; Mason et al. 2022). However, those resource tracking vectors have different diets and may respond to variation in food resources (Blendinger et al., 2015; Fuentes, 1994; Johnson et al., 1985). Moreover, generalist vectors can seek out and subsequently disperse rare fruiting plants (Carlo & Morales, 2016). As a result, resource tracking may result in a positive relationship between the richness of resources and seed rain. Depending on subsequent post-dispersal interactions and microsite quality associated with such vector-preferred resources, this relationship could result in positive feedback that supports diversity in diffuse mutualisms (Gleditsch et al., 2017; Herrera, 1985; Kissling et al., 2007; Mason et al., 2022; Morán-López et al., 2017; Salazar et al., 2013; Spiegel & Nathan, 2010). Meanwhile, shifting food resources as a result of climate change, plant invasions, land cover alteration, harvesting, and shifting disturbance regimes (Boyle et al., 2012; Damschen et al., 2019; Fricke & Svenning, 2020; Gleditsch & Carlo, 2011; McConkey & O’Farrill, 2016; McKinney & Lockwood, 1999; Moegenberg & Levey, 2003; Mollot et al., 2017; Newman, 2019; Rojas et al., 2019), may influence resource tracking and thus seed dispersal (McConkey & O’Farrill, 2016). Predicting how global change can affect vector behavior thus requires understanding how resource richness modulates resource tracking and subsequent patterns of seed dispersal.

We utilized bird feeders as a tool in two experiments to examine how manipulating the richness of food resources influenced 1) the richness and count of birds visiting feeders and 2) the richness and count of seeds deposited beneath feeders. We selected this model system because bird feeders provide a convenient approach to manipulating resource availability, are known to influence bird behavior as resources do, and are ubiquitous in the United States (Cowie & Hinsley, 1988; Fuller et al., 2008; Galbraith et al., 2015; Lepczyk et al., 2004). In the first experiment, we sought to establish the relationship between resource availability and vectored seed dispersal. In the second experiment, we measured how differing levels of resource richness influences this relationship. We expected that increasing the number of resources would lead to more bird counts and greater bird species richness at feeders, generating corresponding patterns in seed rain.

**METHODS**

Experiment 1.

*Location and design.*

We conducted the initial field experiment in a mixed upland forest in southwest Alabama (32°34’10”N, 87°57’04”W) to demonstrate that resources attract seed vectors and subsequent seed rain. Northern Cardinals (*Cardinalis cardinalis*) were the most common dispersers on the property, and our target plant species was yaupon holly (*Ilex vomitoria*). We randomly placed five pairs of bird feeders (18 x 20 x 23 cm, Ogrmar Hanging Gazebo) approximately 100 m apart in open areas bordering brush. Each pair consisted of one feeder stocked with black oil sunflower seeds (*Helianthus annuus*) while the other remained empty. We placed the feeders on an artificial perch above seed traps that we constructed by affixing 0.5 m2 of mesh screening attached to a frame made from wooden slats. In February 2018, we ran two 14-day trials. After the first trial, we collected seeds from the seed trap and switched the treatments within the pair.

*Statistical analysis.*

We analyzed seed arrival at traps in R (R Core Team 2022) with an alpha value of 0.05 (as were all statistical analyses for this paper) using the glmer.nb function to fit a generalized linear model with a negative binomial sampling distribution via maximum likelihood (Bates et al., 2015). We treated resources (baited or empty feeders) and sampling period (1 or 2) as fixed effects, and we included pair (1–5) as a random effect to account for within-pair variation and pseudoreplication (i.e., sacrificial pseudoreplication). The resultant model was formulated as

*(eq. 1)*

where is the negative binomially distributed count of seeds in , is the expected value for that sample in , and is the so-called scaling parameter of the negative binomial distribution (equation 1). We employ the log-link function such that the (hereafter, “ln”) transformed value of the expected count (; equation 2) in pair is a linear function of the predictors, i.e.,

*(eq. 2)*

where is the intercept value, are the parameter estimates, is the treatment variable for pair , is the sampling period variable for pair , and is a random-effects intercept for each pair that accounts for pair-specific variation in seed count. We then used the model output to calculate the estimated marginal means and confidence intervals using the emmeans function (Lenth et al., 2022). We also assessed model fit using analysis of variance (Type II) and by calculating the explained variance (e.g., delta, lognormal, and trigamma methods) using the r.squaredGLMM function (Bartoń, 2022). We had one value associated with baited feeders that was an order of magnitude greater than the rest of the upper quantile. We took a conservative approach and removed the pair from that sampling point and conducted the model again.

Experiment 2.

*Location and design.*

In 1980, the Nature Conservancy and the University of Florida combined 9,500+ acres of diverse vegetation communities in North Central Florida (29°40’22”N, 82°01’58”W), which have been carefully manipulated by land managers and scientists studying environmental responses to stimuli for over 40 years. This research station, known as Ordway-Swisher Biological Station (OSBS), is a mosaic of carefully managed marshes, oak hardwoods, pine flatwoods, and old-field habitats in temperate climate conditions. We established 10 blocks in old fields containing vegetation profiles of primarily grasses and herbaceous plants and 2 blocks in later successional stages with overstories of pines or successional hardwoods. We spaced blocks approximately 1 km away from one another. During the set-up of traps, we recognized signs of wildlife utilizing the old-field blocks, which included: whitetail deer (*Odocoileus virginianus*), common raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), squirrels (*Sciurus spp.*), wild turkeys (*Meleagris gallopavo*), mice (*Apodemus* spp.), snakes (Serpentes), and various small perching birds (Passeriformes).

In each block, we placed four seed traps in the corners of a 10 x 10 m square. We constructed the traps out of 2.54 cm diameter plastic piping, zip-ties, pool screen mesh, wooden dowels, and bird feeders. Each trap consisted of a horizontal 1 x 1 m mesh screen zip-tied to a plastic pipe frame elevated 1 m off the ground by four pipe legs. We suspended each bird feeder above the mesh screen square with a wooden dowel rod horizontally mounted to two vertical 2 m plastic pipes (Figure 1A). The Ogrmar Hanging Gazebo Wild Bird Feeders that we used had dimensions of 18 x 20 x 23 cm and an internal volume of approximately 1.3 L. We labeled each trap with both a trap identification number and its corresponding bird feeder identification number, which was unique to each labeled bird feeder.

Each of our blocks had treatments of zero, four, eight, and twelve resources within bird feeders. Resources we used in the experiment included: wheat (*Triticum* sp.), rye (*Secale cereale*), brown top millet (*Urochloa ramosa*), white millet (*Panicum miliaceum*), oats (*Avena* sp.), black oil sunflower seeds (*Helianthus annuus*), barley (*Hordeum vulgare*), safflower (*Carthamus tinctorius*), cracked corn (*Zea mays*), Nyjer (*Guizotia abyssinica*), peanuts (*Arachis hypogaea*) and black soldier fly larvae (*Hermetia illucens*). To avoid introducing non-native species to the research sites, we heat-treated seeds and nuts to diminish viability and conducted germination tests to examine treatment efficacy. Our heat treatment method consisted of heating seeds with oil contents of 20–60% at 103°C for 17–24 hours and with oil contents below 20% at 130–135°C for 2-4 hours. We tested for germination by placing 20 heat-treated and untreated seeds in damp paper towels within resealable plastic bags stored in dark, room-temperature conditions for 3 weeks. None of our heat-treated seeds germinated. We used program R (R Core Team, 2022) to randomly select and assign unique resource combinations for treatments at each block. Then, we used measuring cups to consistently produce a volume of 0.95 L of resources within each bird feeder (Figure 1B), and we stocked control feeders with natural debris and lined the inside with dull-colored construction paper. At each site, we used a random number generator to assign the placement of treatment levels.

We equipped each seed trap with a Bushnell Trophy Trail Camera to detect bird activity. We positioned all cameras using tripods 1.14 m from the edge of the seed trap, with the camera lens aligned horizontally and vertically with the bird feeder (approximately 1.50 m above the soil surface; Figure 1A). We placed all cameras facing north or south to minimize non-bird stimulus from setting off camera traps depending on block-specific conditions, such as roads or vegetation. We set each trap to high sensitivity with a 10-minute return interval and 15-second video recording at 720 x 1080-pixel image resolution.

We sampled all 40 seed traps five times between 2020-11-27 and 2021-02-03. The first three samples occurred weekly, and the final two sampling dates occurred after a 22- and then 32-day interval (i.e., sampling periods are uneven and sample length is confounded with time since the start of the experiment). Our sampling protocol involved visiting each trap, collecting bird scat and loose seeds located anywhere on the trap structure, and placing collections into a labeled resealable plastic bag. In our sampling protocol, “loose seeds” were seeds not stocked within the bird feeders. Then, we counted and attempted to identify the seed samples. We used these collections to create matrices describing the composition of seed communities within the trap at each time point.

Total seed rain was low in the experiment, and we did not filter seeds according to dispersal mechanism. Although many plant species in our data are not typically associated with dispersal by birds, species of plants with no known adaptation for seed dispersal by animals can still be dispersed by birds (Green et al., 2022). Moreover, due to our experimental design, all traps in a block were exposed to the same ambient seed-rain conditions. We assumed that all traps had an equal chance of receiving seeds from the environment via pathways other than birds, and that birds were driving differences in seed rain. Thus, we included all seeds besides those originating from feeders in our final models. To make sure this approach did not produce misleading results, we ran all seed models with the data filtered to exclude species that were less likely dispersed by birds (Supplemental Materials 1).

While collecting samples, we also swapped out SD memory cards from our trail cameras monitoring the seed traps. We reviewed the videos and recorded the date, species, and quantity of birds in each video clip. Many of the birds recorded at feeders had mainly granivorous or insectivorous diets. However, birds can disperse seeds via several pathways beyond the consumption of fleshy fruit (e.g., endozoochory), such as dyszoochory (seeds dropped before or during ingestion) or epizoochory (seeds externally transported on animals). Moreover, insectivorous or granivorous birds can still eat fruit and disperse seeds (Whelan et al., 2015). Thus, rather than focusing on frugivorous birds, we included all species in our analyses.

*Statistical analysis.*

We determined differences in mean counts and richness for birds and seed rain, and we evaluated potential linear relationships in these response variables as the experiment progressed. We developed a standardized model selection process using general linear models via maximum likelihood:

1. Construct a full model including a random effect for block and an interaction term with a continuous temporal variable.
2. If those models did not converge or performed poorly, replace the random effect for block with a fixed effect.
3. If these models did not converge or performed poorly, drop the interaction term, and construct a model using a categorical temporal variable and a random effect for block.
4. If models perform similarly, choose the model that incorporates the blocked experimental design and interaction term.

We determined the distribution of the data using the descdist function (Delignette-Muller & Dutang, 2015), and we explored model quality with the check\_model function (Lüdecke et al., 2021), the influence function (Nieuwenhuis et al., 2012), and with simulated residuals using the Dharma package (Hartig, 2007). We assessed selected models using type II analysis of variance and by calculating explained variance. We calculated explained variance using the r.squaredGLMM function (e.g., delta, lognormal, and trigamma methods) for mixed effects models (Bartoń, 2022) and McFadden's pseudo-R2 using the pR2 function for models without random effects (Jackman, 2020). Then, we calculated and compared estimated marginal means and trends with confidence intervals and pairwise comparisons using the emmeans, emtrends, and confint functions (Lenth et al., 2022). We reported significant pairwise contrasts derived with and without Holm’s correction for multiple comparisons. If contrasts were significant, we also reported all effect sizes. We reported effect sizes based on Holm’s correction unless the pairwise comparisons were only significant without correction. If models showed collinearity, we reported generalized variance inflation factors calculated using the vif function (Fox & Weisberg, 2019).

2.1 Bird counts.

Before analyzing the data, we filtered out the first two weeks of data to allow for an acclimatization period and summed the total bird detections for each trap by week. We then fit a generalized linear model with a negative binomial sampling distribution for counts of total birds at feeders. Our model included feeder resource level treatment (control = 0, low = 4, medium = 8, or high = 12) and weeks since acclimatization (1–10) as categorical fixed effects and block (1–10) as a random effect (Bates et al., 2015). The regression was formulated as

*(eq. 3)*

where is the negative binomially distributed count of birds detected in block (equation 3), is the expected value for that sample in block , and is the negative binomial distribution’s scaling parameter. The ln transformed value of the expected bird count (; equation 4) in block is a linear function of the predictors, i.e.,

*(eq. 4)*

where is the intercept value, are the parameter estimates, is the treatment variable for block , is the temporal factor variable in block , and is a random-effects intercept for each block that accounts for block-specific variation in bird count (sacrificial pseudoreplication).

2.2 Bird richness.

Again, we removed the initial two weeks of camera trap data to account for an acclimatization period. We used the lmer function to conduct a linear mixed effects model with a Gaussian sampling distribution to assess total bird species richness at feeders across the experiment (Bates et al., 2015). We treated feeder resource level treatment (control = 0, low = 4, medium = 8, or high = 12) and experiment block (1–10) as fixed and random effects, respectively. The regression was expressed as

(*eq. 5*)

where is the normally distributed range of total bird richness observed in (equation 5), is the expected value for that , and is the error parameter for the Gaussian distribution. The expected value for total bird richness (equation 6) in is a linear function of the predictors, i.e.,

(eq. 6)

Where is the intercept value, is the parameter estimate, is the treatment variable for , and is a random-effects intercept for each that accounts for block-specific variation, and thus pseudoreplication in species richness.

We modeled weekly bird richness as a Poisson process using a maximum likelihood approach with the glmer function (Bates et al., 2015). We treated feeder resource level treatment and block as fixed categorical effects and weeks since acclimatization period (1–10) as a fixed continuous effect. The regression was formulated as

*(eq. 7)*

where is the Poisson distributed count of weekly bird richness at block , and is the expected value and variance for that block (equation 7). The ln-transformed value of weekly bird richness (in equation 8) is a linear function of the predictors, i.e.,

*(eq. 8)*

where is the intercept value, are parameter estimates, is the categorical treatment variable at observation , is the parameter estimate for the continuous variable of X since acclimatization at observation , is the interaction term, and is a random-effects intercept for each block that accounts for block-specific variation in weekly bird richness (sacrificial pseudoreplication).

2.3 Seed counts.

We modeled seed counts using the glmer.nb function to fit a generalized linear model with a negative binomial sampling distribution (Bates et al., 2015). We treated resource richness (control = 0, low = 4, medium = 8, or high = 12) and days since start of the experiment (7–75) as fixed categorical and continuous effects, respectively. We included the categorical variable block (1–10) as a random effect to account for within block variation and pseudoreplication (i.e., sacrificial pseudoreplication). The resultant model was formulated as

*(eq. 9)*

where is the negative binomially distributed count of seeds counted in block (equation 9), is the expected value for that sample in block , and is the scaling parameter of the negative binomial distribution. The ln transformed value of the expected seed count ( in equation 10) in block for is a linear function of the predictors, i.e.,

*(eq. 10)*

where is the intercept value, are the parameter estimates, is the treatment variable in block is the continuous variable in block for days since start of experiment, is the interaction term for block , and is a random-effects intercept for each block accounting for block-specific variation in seed count.

2.4 Seed richness.

We used the glmer function to conduct a general linear mixed effects model with a Poisson sampling distribution to assess total seed species richness at feeders across the experiment (Bates et al., 2015). We treated feeder resource level treatment (control = 0, low = 4, medium = 8, or high = 12) and block (1–10) as fixed and random effects, respectively. The regression was expressed as

(*eq. 11*)

where is the Poisson distributed value of total seed richness observed in block, and is the expected value and error term for that block (equation 11). The expected value for total seed richness ( in equation 12) in is a linear function of the predictors, i.e.,

(eq. 12)

Where is the intercept value, is the parameter estimate, is the treatment variable for , and is a random-effects intercept for each that accounts for block-specific variation, and thus, pseudoreplication in species richness.

We analyzed weekly species richness of seed communities arriving in traps using a generalized linear mixed effects model with a negative binomial sampling distribution via the glmer.nb function (Bates et al., 2015). We treated feeder resource level treatment and block as fixed categorical effects and days since start of the experiment as a fixed continuous effect. This model was formulated as

*(eq. 13)*

where is the negative binomially distributed count of seed species detected at block (equation 13), is the expected value for that block, and is the scaling parameter of the negative binomial distribution. The ln transformed value of the expected seed count (; equation 14) is a linear function of the predictor variables, i.e.,

*(eq. 14)*

where is the intercept value, are the parameter estimates of the fixed effects, is the fixed treatment variable for block, is the continuous variable at days since the experiment started for block , and is the feeder resource level treatment and days since start of experiment interaction variable.

**RESULTS**

Experiment 1

In the conservative negative binomial model (i.e., dropping a pair with extreme values at the baited feeder), resource presence (χ2 = 29.39, df = 1, p < 0.001) was a significant predictor of seed arrival but not days since start of experiment (χ2 = 2.50, df = 1, p = 0.114). The fixed (54-62%) and random (13-16%) effects collectively explained 67–78% of the variance in the conservative seed arrival data. We found that mean seed arrival (Figure 2) in baited traps (x̄ = 124.85, LCL = 60.25, UCL = 258.70) was 8.51 times greater (LCL = 3.93, UCL = 18.50, p <0.001) than control traps (x̄ = 14.66, LCL = 6.95, UCL = 30.94). The model without the outlier pair removed produced a similar difference in seed rain with and without resources, but the estimate of mean seed counts for baited feeders was greater (Supplementary Material).

Experiment 2

We recorded 4,863 bird counts across 10 species on our camera traps. The most counted bird species was the chipping sparrow (*Spizella passerina*, 67.3%), followed by Eastern phoebe (*Sayornis phoebe*, 16.6%), Northern cardinal (*Cardinalis cardinalis*; 14.4%), mourning dove (*Zenaida macroura*; 0.8%), pine warbler (*Setophaga pinus*, 0.6%), gray catbird (*Dumetella carolinensis*, 0.2%), and barred owl (*Strix varia*, 0.1%). Red-shouldered hawk (*Buteo lineatus*), Eastern screech owl (*Megascops asio*), and sedge wren (*Cistothorus stellaris*) collectively accounted for less than 0.1% of counts.

We distinguished 26 morphotypes from 123 total seeds in our seed traps, with few instances of identification to family, genus, or species. Based on identification and morphology, wind-dispersed species accounted for two morphotypes (Asteraceae and *Pinus* sp.), and fleshy-fruited endozoochorous species accounted for three (*Parthenocissus quinquefolia*, *Rhus* sp., and *Smilax* sp.). We also collected one epizoochorous seed associated with mammal dispersal (*Desmodium* sp.) and two canopy species (e.g., *Quercus* and *Pinus* spp.). Collectively, the morphotypes that are not typically associated with seed dispersal by bird species detected in our experiment accounted for 45% of the total seed rain. Many of the remaining unidentified morphotypes were small (< 5 mm) hard seeds.

2.1 Bird counts.

Feeder resource level treatment (χ2 = 71.46, df = 3, p < 0.001) and weeks since acclimatization period (χ2 = 77.73, df = 9, p < 0.001) were statistically significant predictors of bird counts at feeders. The random effect of block explained 31–52% of the variance in bird counts. Treatment and weeks since acclimatization explained 16–27% (total explained variance = 47–79%). Weekly bird counts, averaged over all levels of week since acclimatization, were greatest for the medium feeders (x̄ = 5.40, LCL = 1.91, UCL = 15.33), followed by high (x̄ = 4.64, LCL = 1.63, UCL = 13.18), low (x̄ = 3.12, LCL = 1.09, UCL = 8.89), and control (x̄ = 0.67, LCL = 0.23, UCL = 1.97; Figure 3A). With the Holm correction for multiple comparisons, mean weekly bird counts at the control feeder were 0.22 times less than at low (LCL = 0.11, UCL = 0.44, p < 0.001), 0.12 times less than at medium (LCL = 0.06, UCL = 0.25, p < 0.001), and 0.14 times less than at high feeders (LCL = 0.07, UCL = 0.29, p < 0.001); and at low feeders, they were 0.58 times less than at medium (LCL = 0.32, UCL = 1.04, p = 0.042) and 0.67 times less than at high feeders (LCL = 0.37, UCL = 1.20, p = 0.144), and at medium feeders, they were 1.16 times greater than at high feeders (LCL = 0.66, UCL = 2.06, p = 0.482). Without correction, the difference between mean weekly bird counts at low and high feeders was marginally significant (estimate = 0.67, LCL = 0.44, UCL = 1.04, p = 0.072). This model had influential individual observations and blocks.

2.2 Bird richness.

Treatment was not a significant predictor of total bird species richness at feeders in the overall model (χ2 = 5.76, df = 3, p = 0.124). The model explained 86% of the variance in total bird species richness. The random effect of block explained most of the variance (84%), with treatment accounting for the remaining 2%. Mean total richness was greatest in the high and medium feeders (x̄ = 2.7, UCL = 1.84, LCL = 3.56), followed by control (x̄ = 2.4, UCL = 1.54, LCL = 3.26) and low (x̄ = 2.3, UCL = 1.44, LCL = 3.16; Figure 3B). No pairwise contrasts were significant with Holm’s correction for multiple comparisons. Without correcting for multiple comparisons, mean total bird richness at control feeders was 0.3 less than at high and medium (LCL = -0.73, UCL = 0.13, p = 0.165) and 0.1 greater than at low feeders (LCL = -0.33, UCL = 0.53, p = 0.638); and at low feeders, it was 0.4 less than at medium and high feeders (LCL = -0.83, UCL = 0.03, p = 0.068), and at medium and high feeders it was equal (LCL = -0.43, UCL = 0.43, p = 1.000).

We found that feeder resource level treatment (χ2 = 11.21, df = 3, p = 0.011) and weeks since the acclimatization period (χ2 = 16.54, df = 1, p < 0.001) were statistically significant predictors of weekly bird species richness at feeders. The interaction between treatment and weeks was not significant (χ2 = 2.84, df = 3, p = 0.418; SI Figure 1A). The fixed effects in the model explained 4–6% of the variance in the data. The random blocking effect accounted for 26–43% of the variance (29–49% total explained variance). Mean weekly bird richness was greatest at medium feeders (x̄ = 0.87, LCL = 0.52, UCL = 1.46), followed by high (x̄ = 0.82, LCL = 0.49, UCL = 1.38), low (x̄ = 0.75, LCL = 0.44, UCL = 1.26), and control (x̄ = 0.54, LCL = 0.32, UCL = 0.93). With correction for multiple comparisons, mean weekly bird richness at control feeders was 0.73 times less than at low (LCL = 0.48, UCL = 1.11, p = 0.179), 0.62 times less than at medium (LCL = 0.42, UCL = 0.93, p = 0.012), and 0.66 times less than at high feeders (LCL = 0.44, UCL = 1.00, p = 0.043); and at low feeders, it was 0.86 times less than at medium (LCL = 0.59, UCL = 1.24, p = 0.814) and 0.91 times less than at high feeders (LCL = 0.63, UCL = 1.33, p = 1.00); and at medium feeders, it was 1.07 times greater than at high feeders (UCL = 0.74, UCL = 1.53, p = 1.000). Without using the Holm method for multiple comparisons, the difference in mean weekly bird richness between control and low feeders was significant (estimate = 0.73, LCL = 0.53, UCL = 0.99, p = 0.045).

The coefficient for week since acclimatization was greatest for high-richness feeders (estimate = 0.10, LCL = 0.03, UCL = 0.17), followed by low (estimate = 0.09, LCL = 0.02, UCL = 0.16), medium (estimate = 0.07, LCL = 0.01, UCL = 0.14), and control feeders (estimate = 0.01, LCL = -0.07, UCL = 0.09; SI Figure 1B). No pairwise were significant with or without correcting for multiple comparisons.

In the weekly bird richness model, the simulated residuals deviated from expected distribution (D = 0.08, p = 0.018). Feeder resource treatment and the interaction between treatment and weeks since acclimatization exhibited collinearity (corrected variance inflation factor for treatment = 2.36, weeks since acclimatization = 2.34, interaction term = 2.65).

2.3 Seed counts.

Feeder resource level was not a significant predictor of total seed counts (χ2 = 0.84, df = 3, p = 0.839), but days since start of the experiment (χ2 = 11.67, df = 1, p < 0.001) and the interaction between days since start and feeder resource level were (χ2 = 10.01, df = 3, p = 0.019; SI Figure 1C). Collectively, the model explained 6–41% of the variance in the data. The fixed effects accounted for 3–22% of this variance, with the remaining 3–19% attributable to the random effect of block. Mean seed counts were highest for the medium feeders (x̄ = 0.45, LCL = 0.20, UCL = 1.01), followed by low (x̄ = 0.42, LCL = 0.19, UCL = 0.92), high (x̄ = 0.32, LCL = 0.13, UCL = 0.75), and control (x̄ = 0.25, LCL = 0.10, UCL = 0.58). No pairwise comparisons of mean seed counts were significant with or without correcting for multiple comparisons (Figure 3C).

The interactive effect of days since start of the experiment was greatest for high feeders (estimate = 0.044, LCL = 0.020, UCL = 0.068), followed by medium (estimate = 0.029, LCL = 0.006, UCL = 0.052), low (estimate = 0.023, LCL = -0.002, UCL = 0.048), and control feeders (estimate = -0.020, LCL = -0.052, UCL = 0.011; SI Figure 1D). With Holm’s correction for multiple comparisons, the interactive effect on mean seed counts at control feeders was 0.064 less than at high (LCL = -0.118, UCL = -0.010, p = 0.011), 0.049 less than at medium (LCL = -0.102, UCL = 0.003, p = 0.068), and 0.043 less than at low feeders (LCL = -0.098, UCL = 0.012, p = 0.149); and at low feeders, it was 0.006 less than at medium (LCL = -0.050, UCL = 0.038, p = 0.752) and 0.021 less than at high feeders (LCL = -0.066, UCL = 0.025, p = 0.701); and at medium feeders, it was 0.015 less than at high feeders (LCL = -0.058, UCL = 0.029, p = 0.752). Without Holm’s correction for multiple comparisons, the difference in the interactive effect was significant between control and low (estimate = -0.043, LCL = -0.084, UCL = -0.003, p = 0.037) and control and medium feeders (estimate = -0.049, LCL = - 0.089, UCL = -0.010, p = 0.014; SI Figure 2D).

The residuals for this model were positively skewed, and the simulated residuals deviated from the expected distribution (D = 0.10, p = 0.034). The model terms exhibited collinearity (corrected variance inflation factor for treatment = 1.70, days since start of experiment = 2.51, and interaction term = 2.08). The model based on the filtered data (e.g., no wind-dispersed, canopy, or epizoochorous seeds) produced similar results (Supplementary Materials).

2.4 Seed richness.

Treatment was not a significant predictor of total seed richness (χ2 = 4.64, df = 3, p = 0.201). The entire model explained 18–29% of the variance in total seed rain richness. The fixed effect of treatment explained 8–13% of this variance, with the random effect of block accounting for the remaining 10–17%. Mean total seed richness was greatest at high and medium feeders (x̄ = 1.69, LCL = 1.00, UCL = 2.85), followed by low (x̄ = 1.03, LCL = 0.55, UCL = 1.96) and control feeders (x̄ = 0.85, LCL = 0.42, UCL = 1.70; Figure 3D). With Holm’s correction for multiple comparisons, the differences between total seed richness at feeders were not significant. Without correcting for multiple comparisons, total species richness at high feeders was 2.00 times greater than at control (LCL = 0.90, UCL = 4.43, p = 0.087), 1.63 times greater than at low (LCL = 0.78, UCL = 3.45, p = 0.195), and equal to medium feeders (LCL = 0.52, UCL = 1.91, p = 1.000); and at control feeders, it was 0.82 times less than at low (LCL = 0.34, UCL = 1.96, p = 0.653) and 0.50 times less than at medium feeders (LCL = 0.23, UCL = 1.11, p = 0.087); and at low feeders, it was 0.61 times less than at medium feeders (LCL = 0.29, UCL = 1.29, p = 0.195). This model exhibited quantile deviations between simulated residuals and predicted variables (p < 0.001) and there were influential observations.

Resource richness treatment was not a significant predictor of mean seed richness per sample (χ2 = 1.44, df = 3, p = 0.697), but days since the start of the experiment (χ2 = 20.27, df = 1, p < 0.001) and the interaction between treatment and days were (χ2 = 9.70, df = 3, p = 0.021; SI Figure 1E). The fixed effects in the model explained 4–23% of the variance in seed richness per sample, with the random effect of block accounting for 1–7% (5–30% total). Mean seed per sample richness was greatest in medium feeders (x̄ = 0.28, LCL = 0.15, UCL = 0.53), followed by high (x̄ = 0.26, LCL = 0.14, UCL = 0.51), low (x̄ = 0.23, LCL = 0.12, UCL = 0.45), and control feeders (x̄ = 0.18, LCL = 0.09, UCL = 0.38). None of the pairwise comparisons were significant with or without correction for multiple comparisons.

The interactive effect of days since start of the experiment on mean seed richness per sample was greatest for high feeders (estimate = 0.034, LCL = 0.016, UCL = 0.052), followed by medium (estimate = 0.030, LCL = 0.013, UCL = 0.048), low (estimate = 0.018, LCL = -0.002, UCL = 0.038), and control feeders (estimate = -0.022, LCL = -0.055, UCL = 0.010; SI Figure 1F). With Holm’s correction for multiple comparisons, the interactive effect at control feeders was 0.040 less than at low (LCL = -0.092, UCL = 0.011, p = 0.160), 0.053 less than at medium (LCL = -0.103, UCL = -0.003, p = 0.027), and 0.056 less than at high feeders (LCL = -0.106, UCL = -0.006, p = 0.019); and at low feeders, it was 0.012 less than for medium (LCL = -0.048, UCL = 0.024, p = 0.744) and 0.016 less than high feeders (LCL = -0.052, UCL = 0.020, p = 0.744); and at medium feeders, it was 0.004 less than at high feeders (LCL = -0.037, UCL = 0.030, p = 0.785). Without correcting for multiple comparisons, the pairwise contrast between control and low feeders was significant (estimate = -0.040, LCL = -0.079, UCL = -0.002, p = 0.040).

The residuals for the weekly richness model were positively skewed, and the predictors exhibited collinearity (corrected variance inflation factor for treatment = 1.95, days since start of the experiment = 1.24, and interaction term = 2.03). Individual observations and blocks influenced the model outcome. The model based on the filtered data (e.g., no wind-dispersed, canopy, or epizoochorous seeds) produced similar results but with more significant differences in total seed richness (Supplementary Materials).

**DISCUSSION**

Our experiments support our prediction that a positive relationship between food-resource and seed-rain species richness is mediated by resource-tracking avian vectors. Whereas previous research has been grounded in the top-down effect of losing species (e.g., see Cramer et al., 2007; Donoso et al., 2020; Naniwadekar et al., 2019; Pérez-Méndez et al., 2016), we present a bottom-up framework based on the food resources that support diversity in diffuse mutualisms. This framework indicates that naturogenic or anthropogenic global changes that affect the abundance and richness of food resources may have an impact on seed dispersal mutualisms.

We demonstrated increased seed-dispersing bird activity with resource availability, which is consistent with previous studies on resource tracking (Gleditsch et al., 2017). Although overall bird richness was low in our second experiment, we also documented a positive response in weekly vector visits and species richness at feeders with increasing resource options. Previous research indicates that animals participating in diffuse seed dispersal relationships seek diverse resources to maintain healthy nutritional levels, which may incentivize seed vectors to seek rare resources (Amato et al., 2013; Blendinger et al., 2022; Carlo & Morales, 2016). Thus, our results may indicate that increased food resource richness can be effective for recruiting dispersers to sites even without many disperser species in the community. Alternatively, the observed patterns in bird visitations and richness may be explained by competitive interactions among species or individuals at feeders that stabilize total species richness even as visitations increase (Galbraith, 2017; Miller et al., 2017). Collectively, our observations of bird vectors at feeders likely indicate a complex relationship among resource richness, vector diet, and vector interactions that drive the activity of animal communities at food resources.

We observed a positive relationship between the presence of resources and seed rain, which echoes previous work demonstrating the indirect effects of resources and attractive wildlife locations on plant communities (Archibald et al., 2005; Boggess et al., 2021; Carlo & Morales, 2016; Gleditsch et al., 2017; Kwit et al., 2004; Rodríguez-Pérez et al., 2014; Salazaret al., 2013; Mason et al., 2022). Moreover, we demonstrated that resources can gradually indirectly influence plant communities over time by increasing the amount and species richness of seed rain. However, the positive relationship between total seed rain and resource richness increased even as seed counts plateaued at medium resource feeders, which may indicate that high resource richness (e.g., 12 resource species) attract individual vectors with intraspecific traits that encourage the dispersal of more plant species (Zwolak, 2018). Importantly, our resource treatments incorporate a variety of sources (e.g., fruit, seeds, and insects), which more accurately reflects the broad diet of potential avian vectors in our system. The resultant pattern of resource tracking on seed rain thus confirms the expectation that cross-resource type interactions may influence seed dispersal (Gleditsch et al., 2017). As such, resources resulting from community diversity more generally (i.e., beyond fruit producing plants) may also influence seed rain, with potential downstream consequences for plant communities and the interactions they support.

The positive relationship we documented among food-resource and seed-rain species richness indicates that the arrangement and richness of resources is an important determinant of plant dispersal. Increased seed rain richness toward resource-rich location may translate into greater resource and vector species richness, promoting diversity in a diffuse mutualism (Carlo & Morales, 2016; Kissling et al., 2007; Morán-López et al., 2017). However, primary food resources for dispersers (e.g., plant tissues and insects) are changing worldwide with land use conversion, climate change, introduced species, harvesting, and altered disturbance regimes (Boyle et al., 2012; Bowler et al., 2019; Damschen et al., 2019; Gleditsch & Carlo, 2011; McConkey & O’Farrill, 2016; Moegenburg & Levey, 2003; Mollot et al., 2017; Sengupta et al., 2015). For example, invasive species may homogenize local food resources, disrupting resource tracking in animals or reducing the potential species richness of seed rain (Fricke & Svenning, 2020; McKinney & Lockwood, 1999). Over long timescales, such declines in seed rain diversity could have substantial effects on vegetation communities, especially once native seed banks are depleted (Plue et al., 2021). Thus, our evidence indicates that understanding the effects of global change on seed dispersal requires examining resource availability and species richness to supplement the conventional focus on habitat fragmentation and vector assemblages.

Limitations and weak statistical results in our work lead to potentially conflicting conclusions. The small differences in seed rain across resource-richness treatments that we documented could have resulted from contamination in the feeder resources or from mammals (e.g., raccoons) visiting the feeders, both of which would indicate that we did not demonstrate linkage between resource richness and bird-mediated seed dispersal. Moreover, our attempts to assess this linkage are complicated by the identity of the birds and seeds arriving at our traps. Most bird activity was dominated by granivorous and insectivorous species. Similarly, we classified relatively few arriving seeds as belonging to fleshy-fruited plant species. Still, many overlooked dispersers and plants participate in diffuse dispersal mutualisms beyond the frugivorous birds and fleshy-fruited species typically associated with dispersal (Green et al., 2022; Whelan et al., 2015). Even if the relationship between resources and bird-mediated seed dispersal that we demonstrate is indicative of natural processes, the amount of seed rain we observed is unlikely to have a biologically significant impact on communities at the spatial or temporal scales simulated by our experiment. On the other hand, the effect of resource richness on this dispersal mutualism may be stronger than our data indicate but masked by our sampling methodology. We collected data during the dormant season when vector and seed availability is typically lower. Given the positive interactive trends in seed rain among resource richness levels and the time since the start of the experiment, we might expect a stronger positive relationship among resources and seed dispersal with longer experiments or greater exposure to seed or vector diversity. However, our evidence does not address such a scenario. Instead, we provide evidence that should encourage future research exploring the effect of resource diversity on seed dispersal, but we caution against overextrapolation from our results.

Although evidence of resource tracking by seed dispersers is widespread, dispersal research related to global change has often focused on the loss of vectors rather than changes in vector behavior (Gleditsch et al., 2017; McConkey & O'Farril, 2016; Valiente-Banuet, 2015; but see Gleditsch & Carlo, 2011; Moegenburg & Levey, 2003; Sengupta et al., 2015; Rojas et al., 2019). Our work illustrates that frameworks primarily built upon the top-down effects of losing large-bodied vertebrate dispersers may overlook the integral bottom-up role that food resources play in shaping seed dispersal patterns (Bregman et al., 2014; McConkey & O'Farril, 2016). Instead, assessing changes to food resources may provide integral information for efforts to conserve and manage seed dispersal networks. Future research should thus focus on addressing how the role of food resource quality and composition impacts seed dispersal networks, especially in situations where vector food resources are threatened by global change.

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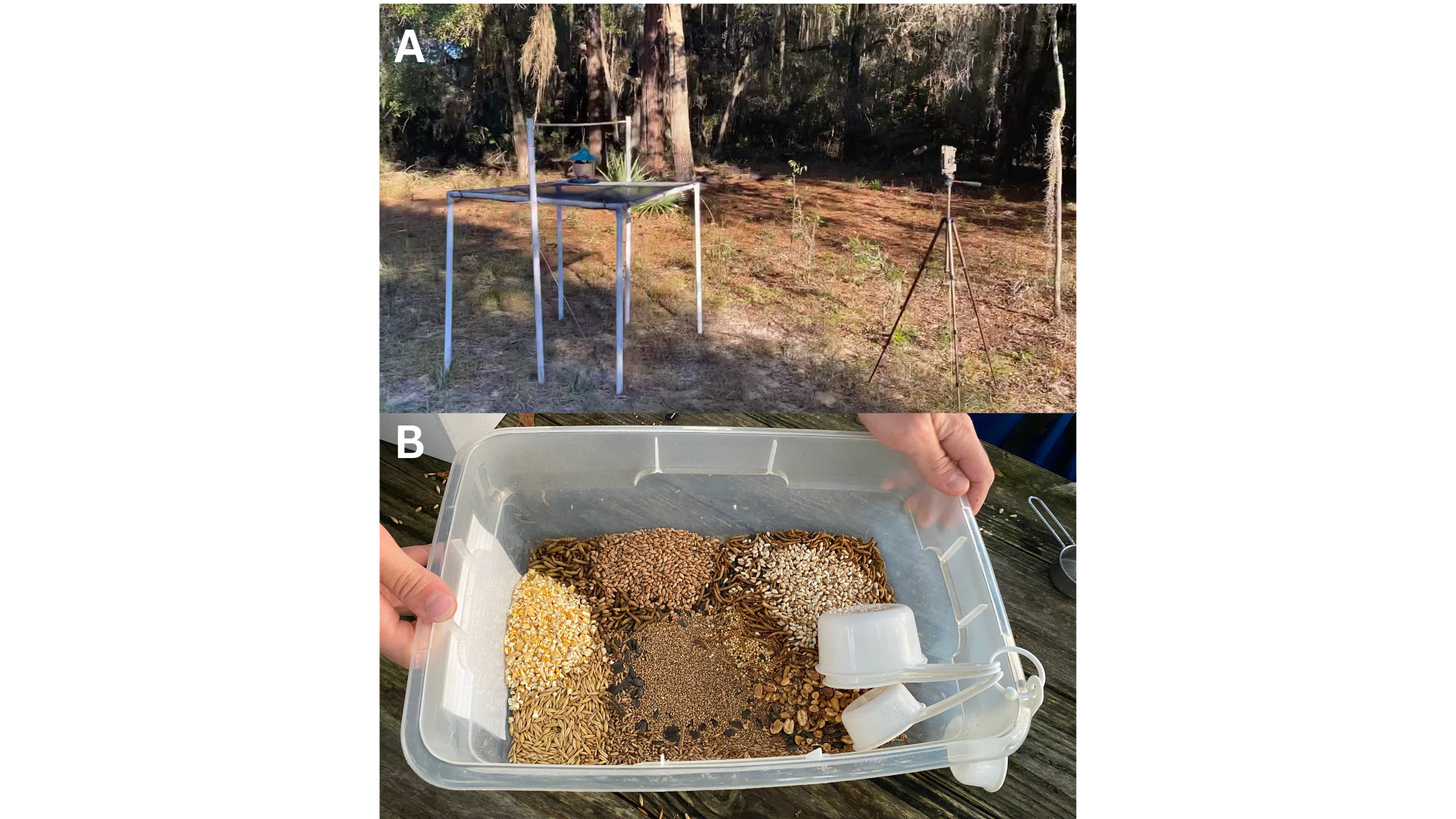
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**Figure 1. Experiment 2 trap design.**

Chart

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**Figure 2. Resources elevate seed rain.**

**Chart, box and whisker chart

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**Figure 3. Resource richness drives patterns in bird visitation and seed rain at traps.**

**Chart, box and whisker chart

Description automatically generated**

**Supplementary Figure 1. The positive relationship between resource richness and seed dispersal by birds increased as the experiment progressed.**

**Figure captions.**

**Figure 1. Experiment 2 trap design.** (A)We paired seed traps beneath feeders with camera traps to simultaneously monitor seed rain and bird activity. (B) We filled baited feeders with 0.95 L of food resources.

**Figure 2. Resources elevate seed rain.** In experiment 1, we compared seed rain beneath baited and empty bird feeders to demonstrate that resources attract vectored seed rain. Mean seed arrival beneath baited traps was 11.5 times greater than that beneath control traps.

**Figure 3. Resource richness drives patterns in bird activity and seed rain.** In experiment 2, we measured how resource richness influenced vectors and seed rain. For the total seed and bird counts, we multiplied means and confidence intervals derived from time-series models by the number of samples. (A) Mean total bird counts at control and low-resource-richness-feeders was lower than at medium and high-resource-richness feeders. Chipping sparrows (*Spizella passerina*) and Eastern phoebes (*Sayornis phoebe*) accounted for 84% of these counts. (B) Mean total bird richness was similar across resource treatments, but weekly bird richness was greater at medium and high-resource-richness feeders than control feeders. (C-D) Similarly, mean total seed count and richness was comparable across treatments but increased throughout the experiment more in medium and high-resource-richness feeders than control feeders. Of the identified and likely bird-dispersed seeds collected from our traps, *Rhus* sp. and *Smilax* sp. arrived at traps most often (14% of total seeds counted). Collectively, these results may indicate that resource richness influences spatial patterns of seed dispersal by birds. Symbols indicate significance levels (i.e., p < 0.10 = +, p < 0.05 = \*, p < 0.01 = \*\*, p < 0.001 = \*\*\*), and the yellow box indicates that the symbol represents significant pairwise comparisons in treatment (i.e., bird richness) or the interaction between time and treatment (i.e., seed counts and richness) in time-series models. Seed images adapted from Tschinkel & Domínguez (2017).

**Supplementary Figure 1. The relationship between resource richness and seed dispersal by birds strengthened as the experiment progressed.** In experiment 2, we explored the interaction between resource richness and time (i.e., days since the start of the experiment for seeds and weeks since acclimatization period for birds). (A) Bird richness increased with weeks since acclimatization at feeders with resources, and (B) the interactive effect did not differ among treatments. (C-D) As time progressed, the number of arriving seeds increased for feeders with resources but decreased for the control feeders, (E-F) and seed rain richness exhibited a similar pattern. Symbols indicate significance levels (i.e., p < 0.10 = +, p < 0.05 = \*, p < 0.01 = \*\*, p < 0.001 = \*\*\*).