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

James P. Holdgrafer1,\*, David S. Mason1, Tyler Steven Coleman2, & Marcus A. Lashley1

1*Department of Wildlife Ecology and Conservation, University of Florida, PO Box 110430, 1745 McCarty Drive, Gainesville, FL, 32611-0410, USA*

2*Florida Cooperative Fish and Wildlife Research Unit, Department of Wildlife Ecology and Conservation, University of Florida, PO Box 110485, 2295 Mowry Road, Gainesville, FL, 32611-0410, USA*

\*Author for correspondence (E-mail: jholdgrafer@ufl.edu; Tel.: (239-220-7414)).

**ABSTRACT:**

1. When acknowledging global change, seed dispersal research mainly focuses on the loss of seed vectors rather than the behavior of existing vectors. Furthermore, many of those studies are conducted in tropical biomes with large-bodied frugivores that are sensitive to habitat fragmentation. In other parts of the world, vertebrate disperser assemblages are robust to fragmentation, but resource tracking may generate consequences for seed dispersal with global change.
2. We hypothesized that diffuse plant-animal dispersal mutualisms are promoted by resource tracking when diverse resources attract different levels of seed rain by different vectors. We expected increasing resource richness to attract more species of vertebrate vectors and subsequently 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 of seed rain and avian vectors present at feeders. Collectively, we observed a positive relationship between available food resources and seed rain, in terms of abundance and richness, mediated by resource tracking of avian vectors.
4. Our findings underscore a key mechanism that may promote diversity whereby accumulating species richness in the plant community attracts greater numbers of species in the seed rain. Importantly, the resource tracking mechanism driving this potential positive feedback loop may also result in negative ecosystem effects if global change alters or homogenizes resource availability. Moving forward, future research in ecosystems where vectors are susceptible to habitat fragmentation should explore the bottom-up effects of global changes on food resources.

*Key words*: *dispersal, diffuse mutualism, seed vector, species richness*

**INTRODUCTION**

Global biodiversity is declining, in part, due to shifts in the availability, distribution, and quality of resources that support ecological interactions (Chapin III et al., 2011; Dirzo et al., 2014; Grime, 1998; G. Miller & Spoolman, 2012; Ricklefs, 2005; Srivastava et al., 2012; Worm et al., 2006). In tropical systems, the persistent progression of human activities continues to diminish the availability and quality of space through habitat loss and fragmentation, creating an asymmetric skew in the loss of biodiversity with the extinction of animals at higher trophic levels and the occurrence of smaller population sizes first (Cramer et al., 2007; Davies et al., 2000; Duffy, 2003; Pérez-Méndez et al., 2016). Such losses raise concerns 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; S. Wang & Loreau, 2016). However, the consequences of global change for seed dispersal mutualisms may differ across ecosystems (Damschen et al., 2019; McConkey & O’Farrill, 2016).

Tropical forest ecosystems represent a disproportionate amount of seed dispersal mutualism research (Davies et al., 2000, 2004; Escribano-Avila et al., 2018; Estrada & Fleming, 1986; C. M. Herrera, 1985), which may bias our general understanding of how global change influences seed dispersal in other ecosystems. In forested tropical ecosystems, asymmetric declines in frugivorous animal populations with habitat fragmentation is hypothesized to negatively impact biodiversity, particularly when some fruits are only dispersed by a subset of dispersers (Carpenter et al., 2018; Carvalho et al., 2021; Case & Tarwater, 2020; Caves et al., 2013; Jordano et al., 2007; Mokany et al., 2014; Naniwadekar et al., 2019; Rumeu et al., 2017). More specifically, the loss of large-bodied frugivores from fragmented landscapes limits dispersal distances and strengthens dispersal limitation, potentially resulting in the loss of functional roles (e.g., large fruit-producing plants; Jordano et al., 2007). However, habitat fragmentation may affect seed dispersal differently in other systems, such as temperate forests, for two reasons. First, most seed dispersal relationships are diffuse mutualisms, defined as a mutually positive relationship including multiple participating species (e.g. pollination, seed dispersal, mycorrhizae; Gove et al., 2007; Rico-Gray, 1993; Stanton, 2003; Zamora, 2000). For example, current temperate ecosystems have fewer fruit-producing species that are dispersed by a subset of large-bodied dispersers than the tropics (Stiles, 1980). Second, temperate forest bird assemblages are more robust to habitat fragmentation than tropical birds (Bregman et al., 2014). This discrepancy between temperate and tropical ecosystems underscores the need to reevaluate seed dispersal processes outside the tropics for a more robust understanding of how different resources affect seed dispersal relationships (Escribano-Avila et al., 2018).

Whereas previous research 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, food resources are particularly influential for seed dispersal in linking broad patterns of frugivore and fruit diversity (García & Ortiz-Pulido, 2004; Gleditsch et al., 2017; Rodríguez-Pérez et al., 2014). The effect of food resources on seed dispersers are often studied using a resource tracking framework (Gleditsch et al., 2017; Jongejans et al., 2015; Rodríguez-Pérez et al., 2014). According to this framework, resources, such as perches (Verdu & Garcia-Fayos, 1996), cover (J. M. Herrera et al., 2011), and fruit (J. M. Herrera et al., 2011; Rodríguez-Pérez et al., 2014), can indirectly attract seed rain by influencing animal behavior (Saracco et al. 2004; García et al., 2011; Carpentar et al. 2018; Schupp et al., 2019). Resource tracking vertebrate vectors have different diets and respond to variation in food resources (Blendinger et al., 2015; Fuentes, 1994; Johnson et al., 1985; McConkey & O’Farrill, 2016). Moreover, generalist vectors 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 ecological interactions and microsite quality associated with such vector-preferred resources, this relationship may result in a positive feedback loop that supports diversity in diffuse mutualisms (Spiegel & Nathan, 2010). However, with food resources shifting in many ecosystems as a result of climate change, plant invasions, land cover alteration, and shifting disturbance regimes (Damschen et al., 2019; Gleditsch & Carlo, 2011; McConkey & O’Farrill, 2016; Mollot et al., 2017), resource tracking may instead result in negative outcomes (i.e., plant community homogenization or introductions). Predicting how global change can influence vector behavior thusly requires understanding how resource richness influences resource tracking and subsequent patterns of dispersal.

We utilized bird feeders as a tool in two experiments to examine how manipulating the richness of food resources available to bird communities influenced: 1) the richness and observations of birds visiting feeders and 2) the richness and observations of seeds deposited beneath feeders through bird excrement. We selected this model system because bird feeders provide a convenient approach to manipulate 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 a relationship between resource availability and vectored seed dispersal. In the second experiment, we explored the effect of differing levels of resource species richness. We expected that increasing the number of resources would lead to more detections and greater species richness of birds at feeders, generating corresponding increases in seed rain.

**METHODS**

*Software.*

All statistical analyses were executed in the programming language R (R Core Team, 2019) using an alpha value of 0.05 to determine statistical significance.

Experiment 1.

*Location and design.*

We conducted the initial field experiment in a mixed upland forest in southwest Alabama (32°34’10.2”N, 87°57’03.6”W) to demonstrate that resources attract seed vectors and subsequent seed rain. Northern Cardinals (*Cardinalis cardinalis*) are 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 (0.18 x 0.20 x 0.23 m, Ogrmar Hanging Gazebo) approximately 100 m apart in open areas bordering brush. Each pair consisted of one feeder stocked with black oil sunflower seeds while the other remained empty. We placed the feeders on an artificial perch above seed traps 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 (n = 20). After the first trial, we collected seeds from the seed trap and switched the treatments within the pair. Then, we collected the seeds after the second 14-day period.

*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). Treatment (baited or empty feeders) and sampling period (1 or 2) were fixed effects. We included pair (e.g., 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 pair (equation 1), is the expected value for that sample in pair , and is the so-called scaling parameter of the negative binomial distribution. 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) and we also assessed the model fit using analysis of variance (Type II) and by calculating the explained variance (e.g., trigamma method; Bartoń, 2022).

Experiment 2.

*Location and design.*

In 1980, the Nature Conservancy and the University of Florida combined 9,500+ acres of diverse ecosystems in North Central Florida (29°40’22”N 82°01’58”), which has 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.

At OSBS, we established ten blocks in old fields containing vegetation profiles of primarily grasses and herbaceous plants and two blocks in further vegetative successional stages with overstories of pine or oak trees. 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 bird scat traps in the corners of a 10 x 10 m square. We constructed scat traps out of 2.54 cm diameter PVC piping, zip-ties, pool screen mesh, wooden dowels, and bird feeders, such that a horizontal 1 x 1 m mesh screen was zip-tied to a PVC pipe frame elevated 1 m off the ground by four PVC pipe legs. We suspended each bird feeder above the mesh screen square by a wooden dowel rod horizontally mounted to two vertical 2 m tall PVC pipes (Figure 1A). The Ogrmar Hanging Gazebo Wild Bird Feeders that we used had dimensions of 0.18 x 0.20 x 0.23 m and an internal volume of approximately 1.3 L. We labelled each trap with both a trap identification number and its corresponding bird feeder identification number unique to each labelled bird feeder.

Each block had treatments of zero, four, eight and twelve resources within bird feeders. Resources 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, seeds and nuts used for resources were heat-treated to destroy viability and underwent germination tests to examine treatment efficacy. Heat treatment consisted of heating seeds and nuts with oil contents of 20-60% at 103°C for 17-24 hours and nuts and seeds with oil contents below 20% at 130-135°C for 2-4 hours. Germination tests consisted of placing 20 heat-treated and untreated seeds or nuts in damp paper towels within Ziploc bags stored in dark, room-temperature conditions for 3 weeks. None of the heat-treated seeds germinated. We used program R (R Core Team 2022) to randomly select and assign the resources used for each treatment at each site from a list of 12 different resources. Measuring cups were used to consistently produce a volume of 4 cups of resources within each bird feeder (Figure 1B). At each site, a random number generator assigned the placement of the four treatment levels to the four traps.

Each bird scat trap was equipped with a Bushnell Trophy Trail Camera to detect bird activity. All cameras used were positioned on tripods 1.14 meters from the edge of the scat trap, with the camera lens at the same level as the center of the bird feeder (approximately 1.50 meters above the ground; Figure 1A). All cameras at each site were facing north or south. The direction was decided depending on site-specific conditions, such as roads or vegetation, to minimize non-bird stimulus from setting off camera traps. Each trap was set to high sensitivity with a 10-minute interval and 15 second video recording at 720 x 1080 pixel image resolution.

All 40 scat traps were sampled weekly from 11/20/2020 to 01/31/21. Sampling protocol involved visiting each trap, collecting bird scat and loose seeds located anywhere on the trap structure and placing collections into a labelled resealable plastic bag. In our sampling protocol, loose seeds were seeds not stocked within the bird feeder of the trap being sampled. These seeds were assumed to arrive through scat washed away by rain. At the lab, seeds from samples were counted and identified. These collections were used to create matrices describing the composition of seed communities within the trap at each time point.

*Statistical analysis.*

2.1 Bird counts.

Before analyzing data, we filtered out the first two weeks to allow for an acclimatization period for birds at feeders. We then fit a generalized linear model with a negative binomial sampling distribution via maximum likelihood for counts of total birds counted (i.e., detected) at feeders, including feeder resource level treatment (control = 0, low = 4, medium = 8, or high = 12 resources) as a categorical fixed effect and block 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, is the parameter estimate, is the treatment variable for block , and is a random-effects intercept for each block that accounts for block-specific variation in bird count (sacrificial pseudoreplication). We then used the model output to calculate the estimated marginal means and confidence intervals using the *emmeans* function (Lenth et al., 2022) and we assessed the model fit by observing the residuals (SI Figure 2), running a type II analysis of variance, and by calculating explained variance (e.g., delta, lognormal, and trigamma method; Bartoń, 2022).

2.2 Bird richness.

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

*(eq. 5)*

*(eq. 6)*

where is the normally distributed range of bird species richness observed in each block (equation 5), is the expected value for that sample in block , is the error parameter for the Gaussian distribution, is the intercept value, is the parameter estimate, is the categorical treatment variable for block , and is a random-effects intercept for each block that accounts for block-specific variation, and thus pseudoreplication, in species richness (equation 6). We assessed the model fit by observing the residuals (SI Figure 3), running an analysis of variance (type II), and examining the explained variance (e.g., delta, lognormal, and trigamma method; Bartoń, 2022). We then calculated and compared estimated marginal means using the emmeans function (Lenth et al., 2022).

2.3 Seed counts. (SI figure 4-5)

We modelled seed counts throughout the experiment using the manyglm function to calculate multivariate generalized linear models with a negative binomial sampling distribution via maximum likelihood (Wang et al., 2022). The manyglm function calculates a global model using all species in the dataset and single models for each species (Wang et al., 2022), i.e.,

*(eq. 7)*

where is the negative binomially distributed count of seeds detected in block for species (equation 7), is the expected value for that sample in block for species , and is the scaling parameter of the negative binomial distribution. The ln transformed value of the expected seed count (; equation 8) in block for species is a linear function of the predictors, i.e.,

*(eq. 8)*

where is the intercept value, are the parameter estimates of the fixed effects, is the treatment variable in block for species , is the sampling period variable in block for species , and is a random-effects intercept for each block and species that accounts for block-specific variation in seed count (sacrificial pseudoreplication). It is important to note that the global model included all seed species, therefore removing from equations 7 and 8. We assessed the model fit by observing the each models predicted residuals compared to the original data and by using the function manyglm.anova (e.g., see Wang et al., 2022).

2.4 Seed richness.

We analyzed the 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). This model was formulated as

*(eq. 9)*

where is the negative binomially distributed count of seed species detected 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 (; equation 10) in block is a linear function of the predictor variables, i.e.,

*(eq. 10)*

where is the intercept value, are the parameter estimates of the fixed effects, is the fixed treatment variable in block , is the fixed sampling period variable in block , \* is the feeder resource level treatment and sampling period interaction variable in block , and is a random-effects intercept for each block that accounts for experimental block-specific variation in seed species richness (sacrificial pseudoreplication). We assessed the model fit by observing the residuals (SI Figure 6-7) and by conducting an analysis of variance (Type II), calculating explained variance (e.g., delta, lognormal, and trigamma method;(Bartoń, 2022), and estimating marginal means and trends (e.g., coefficient estimates) with confidence intervals using the emmeans package (Lenth et al., 2022).

**RESULTS**

Experiment 1

Resource level (χ2 = 41.1914, df = 1, p < 0.001) and sampling period (χ2 = 7.5171, df = 1, p < 0.006) were statistically significant predictors of seed arrival (i.e., count), collectively accounting for 57% of model variance. The random effect of pair explained 17% of the remaining variance in seed arrival (74% total). We found that mean seed arrival (Figure 2) in baited traps (x̄ = 162; 70.74–369.1, ±95% CI) was 11.5 times greater than control traps (x̄ = 14, LCL = 6.07, UCL = 32.3).

Experiment 2

2.1 Bird counts.

Feeder resource level treatment was a statistically significant predictor of total bird detections at feeders (Figure 3A; χ2 = 25.6, df = 3, p < 0.001). The random effect of block explained 70-74% of the variance in bird detections. Treatment explained 14-15% (total explained variance 85-89%). Mean total bird detections was greatest for the medium resource feeder (x̄ = 63.2, LCL = 20.6, UCL = 193.3), followed by high resource (x̄ = 58.7, LCL = 19.2, UCL = 180.1), low resource (x̄ = 44.8, LCL = 14.6, UCL = 137.5), and control (x̄ = 10.6, LCL = 3.3, UCL = 34.2). The contrast between the control and medium (ratio = 0.168, p < 0.001), high (ratio = 0.181, p < 0.001), and low (ratio 0.237, p < 0.001) feeder treatments was statistically significant. Here I would add the effect sizes for each comparison (e.g., “We found that the control observed [Beta estimate] more/less birds ([95% CI]; ±95% CI) than low feeder resource levels (p = []), [Beta estimate] more/less birds ([95% CI]; ±95% CI) than medium feeder resource levels (p = []), and [Beta estimate] more/less birds ([95% CI]; ±95% CI) than high feeder resource levels (p = []). The low resource feeder observed [Beta estimate] more/less birds ([95% CI]; ±95% CI) than medium feeder resource levels (p = []) and [Beta estimate] more/less birds ([95% CI]; ±95% CI) than high feeder resource levels (p = []). Lastly, the medium resource feeder observed [Beta estimate] more/less birds ([95% CI]; ±95% CI) than the high resource feeder (p = []).”).

2.2 Bird richness.

We found feeder resource level treatment was a statistically significant predictor of bird species richness at feeders (Figure 3A; χ2 = 7.9, df = 3, p = 0.05). The entire model explained 90% of the variance in the model, but a majority of that was associated with the random effect of block (87%). Bird species richness was greatest at the medium resource feeders (x̄ = 2.8, LCL = 1.93, UCL = 3.67), followed by high (x̄ = 2.7, LCL = 1.83, UCL = 3.57), control (x̄ = 2.4, LCL = 1.53, UCL = 3.27), and low (x̄ = 2.3, LCL = 1.43, UCL = 3.17). The contrast between low and medium feeders was statistically significant (t ratio = -2.412, p = 0.02). The contrast between control and medium feeders (t ratio = -1.930, df = 27, p = 0.06) and low and high feeders (t ratio = -1.930, df = 27, p = 0.06) was marginally statistically significant. I would add the effect sizes for each comparison just like above.

2.3 Seed counts.

Treatment (Res.df. = 196, Df.diff = 3, Test statistic = 99.39, p = 0.06) and sampling period (Res.df = 195, Df.diff = 1, Test statistic = 122.06, p = 0.001) were statistically marginal and significant predictors of seed detections in the global model, respectively (Figure 3B). However, those patterns of statistical significance from the global model were not reflected with individual species-specific models, with one exception. Sampling date was a statistically significant predictor of sumac species detections in the single-species general linear model (Test statistic = 17.181, p = 0.001). This species was only detected in the final sampling period. I would add the effect sizes for each comparison just like above.

2.4 Seed richness.

The feeder resource level treatment and sampling period interaction effect (χ2 = 11.9069, df = 3, p < 0.008) and sampling period effect (χ2 = 9.3373, df = 1, p < 0.002) were statistically significant predictors of species richness of seeds arriving at traps. The effect of the feeder resource level treatment alone was not statistically significant (χ2 = 2.1257, df = 3, p < 0.547). Collectively, the fixed effects accounted for 4-24% model variance. The random effect of experimental block explained 4-26% of the remaining variance in seed arrival (8-50% total). The mean arrival of each treatment did not significantly differ statistically (SI Table 1). However, sampling period influenced treatments differently. The effect of sampling period on control (estimate = -0.668, LCL = -0.822, UCL = 0.0875) did not significantly differ from low resource level treatment (estimate = 0.301, LCL = -0.110, UCL = 0.7123, p = 0.142) but did for medium (estimate = 0.494, LCL = 0.127, UCL = 0.8615, p = 0.02), and high (estimate = 0.619, LCL = 0.230, UCL = 1.0081, p = 0.007) resource level treatments (Figure 3B).

**DISCUSSION**

We found evidence for a positive relationship among food resource and seed rain species richness mediated by resource tracking avian vectors. Whereas copious previous research is grounded in the top-down effect of losing species (e.g., see Mokany et al., 2014; Naniwadekar et al., 2019), we present a bottom-up framework built on the food resources that support diversity in diffuse mutualisms. This framework indicates that global changes—naturogenic or anthropogenic—adjusting the distribution and diversity of food resources may impact seed dispersal mutualisms.

We demonstrated increased bird activity with greater resource availability, which is consistent with previous studies on resource tracking (Gleditsch et al., 2017; Kwit et al., 2004). However, we observed bird behavior seeking diverse resources resulted in higher bird species richness at feeders with greater food resource species richness, but not more bird detections overall. 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, this discrepancy between bird detections and richness may indicate that increased food resource richness can be effective for recruiting diverse disperser communities to sites, but that individuals may not require multiple feeding events at a single feeder to achieve the desired benefit (Bergman et al., 2001; Carlo & Morales, 2016). Alternatively, the observed patterns in bird activity may be explained by competitive interactions among species or individuals at feeders that stabilize overall activity even as species richness increases (Leighton et al., 2022; E. T. Miller et al., 2017). Collectively, our observations of bird vectors at feeders likely indicate a complex relationship among resource tracking, vector diet, and ecological interactions that drive the activity of animal communities associated with food resources.

We observed a positive relationship among the presence of resources and seed rain, which echoes previous work demonstrating the indirect effects of resources on plant communities (Archibald et al., 2005; Carlo & Morales, 2016; Hempson et al., 2017; Schmidt, 2003). Moreover, we demonstrated that resources can indirectly influence plant communities by increasing the species richness of seed rain. The positive relationship between seed rain and resource richness increased even as bird detections and richness plateaued. We observed relatively low species richness of bird vectors at low resource richness feeders (e.g., 4 resource species), which indicates that high resource richness (e.g., 12 resource species) may instead attract individuals that disperse more plant species (Zwolak, 2017). Importantly, the strength of this positive relationship between resource and seed rain species richness increased throughout the sampling period. Temporal patterns (i.e., seasonal variation or acclimatation) are important factors in resource tracking frameworks, which often focus on fruit availability at neighborhood or landscape scales (Gleditsch et al., 2017). Instead, our results incorporate community diversity more generally (e.g., fruit, seeds, and insects), which more accurately reflects the generalist diet of most vectors (Gleditsch et al., 2017). As such, the effect of community diversity on temporal variation in resource tracking may dictate seed rain, with downstream consequences for plant community assembly and other interactions (e.g., seed predation; Howe & Miriti, 2004; Lishawa et al., 2020).

The positive relationship we documented among food resource and seed rain species richness raises concerns regarding resource fluctuations with global change. Increased seed rain species richness may translate into greater resource and vector species richness, promoting diversity in a diffuse mutualism (Palmer et al., 2003). However, primary food resources for dispersers (e.g., plant tissues and insects) are declining or shifting worldwide with land use conversion, climate change, introduced species, and altered disturbance regimes (Bowler et al., 2019; Damschen et al., 2019; Gleditsch & Carlo, 2011; McConkey & O’Farrill, 2016; Mollot et al., 2017). For example, invasive species may homogenize food resources in areas, decreasing resource tracking in animals or reducing the potential species richness of seed rain (Fricke & Svenning, 2020). Over long timescales, such declines in seed rain diversity could have substantial effects on vegetation communities once native seed banks are depleted (Plue et al., 2021). Thus, a thorough understanding of 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.

Our work has limitations that may restrict the generalizability and strength of the findings. We detected few seeds in our second experiment, which may have obscured the effect of resource availability on seed rain by limiting variation in seed rain diversity. Moreover, the bird community detected on camera traps was depauperate. Collectively, these limitations may have limited the effect size of resources on bird and seed rain species richness. Still, small effect sizes are not unusual for indirect relationships (Wootton, 2002), and weaker statistical significance does not make a relationship unimportant. Indeed, indirect effects in diffuse mutualisms can play a large role in shaping ecosystems, especially when occurring across landscapes and over evolutionary timescales. However, we do caution against extrapolation from our findings. Although we expect the same positive relationship among resources and seed dispersal with resource tracking across systems, we do not provide evidence that directly informs situations with greater seed rain or vector diversity. Similarly, the season when sampling occurred (dormant) likely influenced the observed patterns, but annual temporal variation was outside the scope of our design. Despite these limitations, we provide evidence for a relationship linking community diversity to a key ecosystem service via resource tracking by vectors in a diffuse mutualism.

There is widespread evidence of resource tracking by seed dispersers; however, dispersal research has focused mostly on the loss of vectors rather than changes in vector behavior (Moore & Swihart, 2007; Mubamba et al., 2022). Our work illustrates that conservation efforts primarily built upon the top-down effects of losing large-bodied vertebrate dispersers may overlook the integral bottom-up role food resources play in attracting seed vectors in ecosystems (Bregman et al., 2014). Moving forward, assessing changes to food resources may provide integral information for efforts to conserve and manage seed dispersal networks. Future research should focus on experimentally addressing how the role of food resource quality and composition shifts across context, with special focus on food resources that are threatened by global change.

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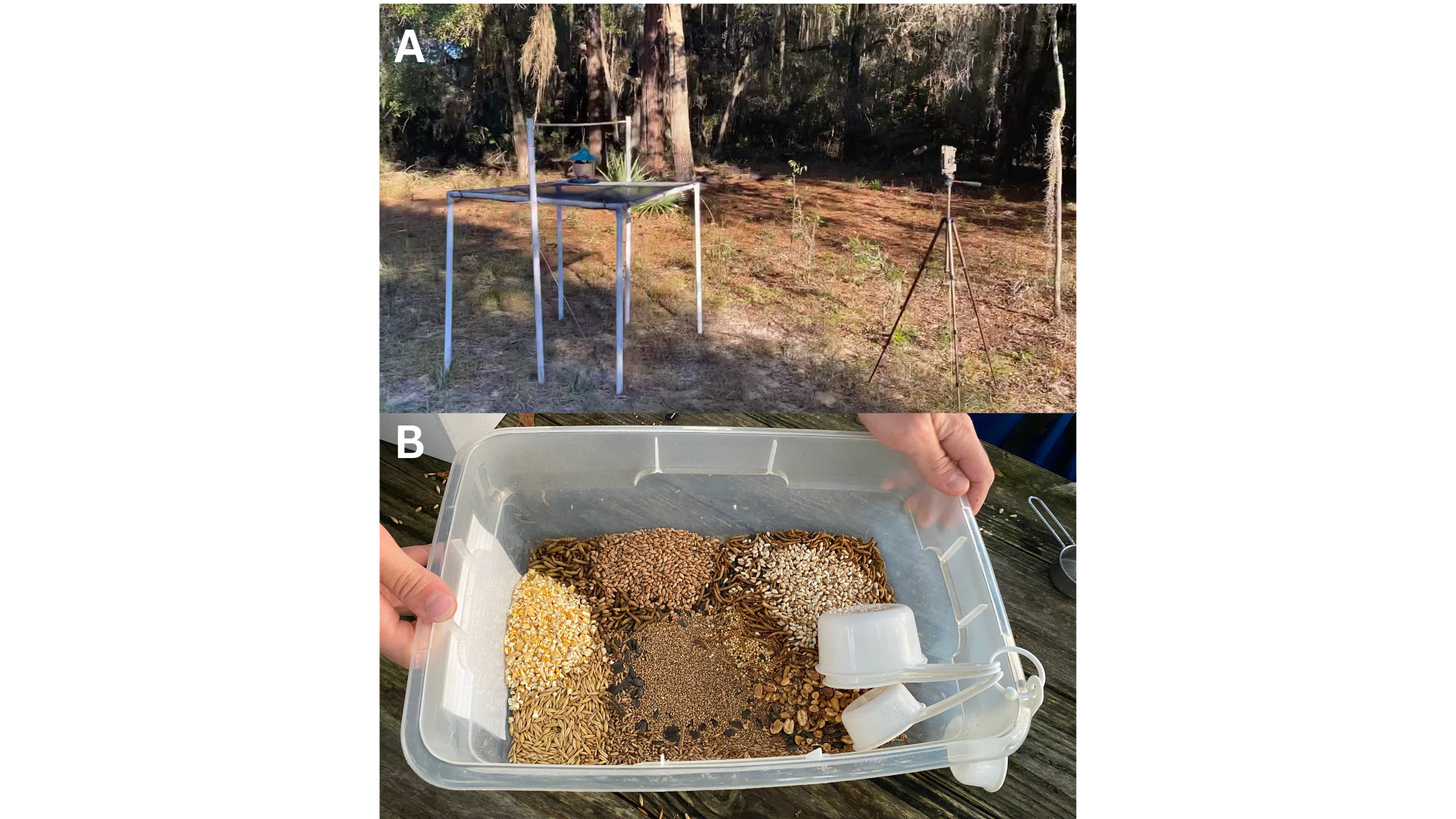
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**Figure 1. Experiment 2 trap design.** (A)We designed and constructed seed traps to capture seeds deposited by vectors attracted to food resources inside bird feeders. Each seed trap was equipped with a camera trap to monitor wildlife use. (B) Each bird feeder was filled with 4 cups of food resources, except for control treatments. Resources stocked in each feeder were assigned using a random generator and were measured using standard measuring cups.

Chart

Description automatically generated

p < 0.001

**Figure 2. Resources elevate seed rain.** In experiment 1, we compared the seed rain beneath baited and unbaited bird feeders. Mean seed arrival in baited traps was 11.5 times greater than control traps.

**Chart, box and whisker chart

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**Figure 3. Resource richness drives patterns in bird activity and seed rain at traps.** In experiment 2, we examined how the species richness of resources (none, low, medium, and high) influenced the detections (counts) and species richness of vectors and seed rain at feeders. (A) Feeder resource level treatment was significant predictor of bird detections and species richness at feeders. (B) Treatment and sampling period were marginal and significant statistical predictors of seed detections. The interaction between the feeder resource level treatment and sampling period were statistically significant predictors of richness in the community of seeds arriving at traps. We need to explain what the asterisks significance specifically represents. Also need to explain what the species on the right represent. I am not sure those are needed although I do find them visually appealing.

**Supplementary Table 1.** Comparison of the emmeans function results from seed species richness analyzed with a generalized linear mixed effects model. The Z ratio represents…

|  |  |  |
| --- | --- | --- |
| Contrast | z.ratio | p-value |
| Control / Low | -0.389 | 0.6975 |
| Control / Medium | -1.097 | 0.2728 |
| Control / High | -0.917 | 0.3594 |
| Low / Medium | -0.733 | 0.4637 |
| Low / High | -0.552 | 0.5810 |
| Medium / High | 0.164 | 0.8699 |

**Diagram, engineering drawing

Description automatically generated**

**Supplementary Figure 1. Model validation for experiment 1.**

**Diagram

Description automatically generated**

**Supplementary Figure 2. Validation for bird detection model from experiment 2.**

**Diagram

Description automatically generated**

**Supplementary Figure 3. Validation for bird richness model from experiment 2.**

**Chart, line chart

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**Supplementary Figure 4. Seed detections by sampling period.** Need to explain the x- and y-axes and what the colors represent. Also, make sure the colors are labelled correctly and match figure 1 after figure 1 is corrected.

**Chart, scatter chart

Description automatically generated**

**Supplementary Figure 5. Validation for seed detection model for experiment 2.** What do the colors represent?

**Chart, line chart

Description automatically generated**

**Supplementary Figure 6. Seed richness changes across time.** Explain the figure.

**Diagram, engineering drawing

Description automatically generated**

**Supplementary Figure 7. Validation for seed richness model from experiment 2.**