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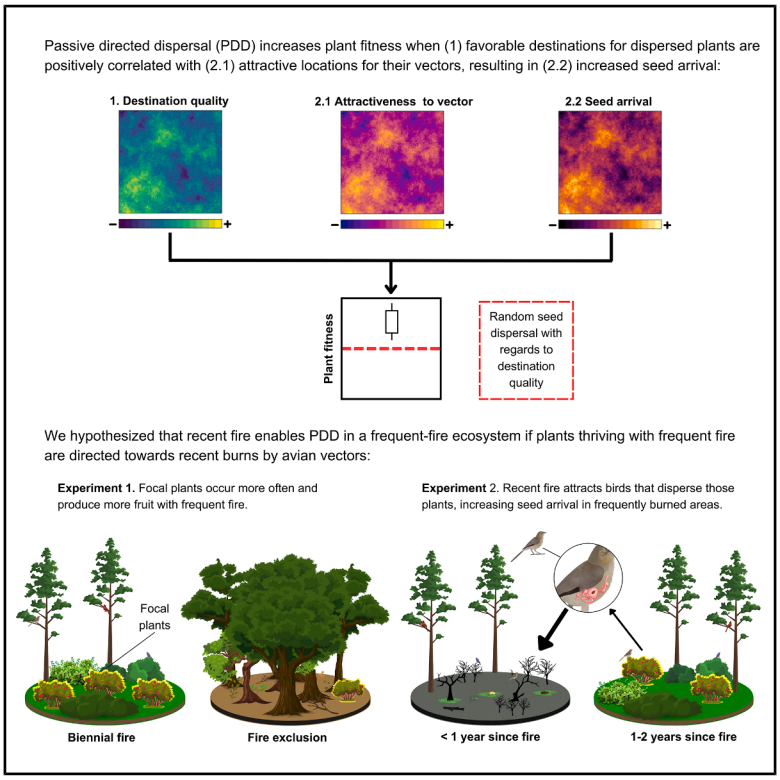
Current Biology

Fire enables passive directed seed dispersal by birds

Graphical abstract



Highlights

- PDD occurs when dispersers are attracted to favorable seed destinations
- Recurring fire creates favorable conditions for common bird-dispersed plants
- The magnet effect also directs seeds from those plants to recently burned areas
- This directs plants to areas that burn and offsets fruit deficits and seed loss

Authors

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In brief

Mason et al. show that recent fire attracts bird-mediated seed dispersal of plant taxa that thrive with frequent fire, revealing that passive directed dispersal can result from a global terrestrial phenomenon.

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Fire enables passive directed seed dispersal by birds

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SUMMARY

Recent work proposes that passive directed dispersal (PDD) occurs when resource tracking leads animal vectors to disperse seeds at sites that favor plant establishment. For example, wildland fire can attract seed-dispersing animals via the magnet effect while simultaneously generating the environmental conditions that benefit animal-dispersed plants. To evaluate the hypothesis that frequent fire results in PDD, we first documented the effect of frequent fire on locally common bird-dispersed plants known to be promoted by fire by measuring frequency of occurence along transects and per-individual fruit production in a long-term replicated fire experiment. Two of these focal plant taxa occurred more frequently in plots burned biennially compared with plots that remained unburned for approximately six decades. All focal plant taxa produced more fruit per individual with recurring fire. Next, we used a paired crossover experiment to measure bird activity and bird-dispersed seed rain at perches after fire. Fire increased seed dispersal distance and elevated seed loss from seed traps. When adjusting for these confounding factors, the magnet effect of recent fire resulted in greater projected seed rain from focal plant taxa arriving in recent burns compared with areas burned 1–2 years prior. Collectively, these results suggest that wildland fire generates the necessary conditions for PDD. With the prevalence of fire in terrestrial ecosystems, PDD may thus be a widespread process shaping global plant communities.

INTRODUCTION

One interpretation of the diffuse mutualism paradigm is that directed seed dispersal by animals—defined as nonrandom deposition of seeds at destinations that provide a fitness advantage—is rare.[1] This interpretation arose from the presumption that traits favoring directed seed dispersal evolve within specialized plant-animal dispersal relationships, followed by the recognition that most relationships are instead diffuse.[1] Specialized traits include mistletoe (Santalales) fruit containing a sticky substance that induces vectors to dislodge seeds directly onto suitable host trees and fat bodies on myrmecochorous seeds that encourage ants to deposit seeds in advantageous microsites associated with ant nests.[1] In contrast, Mason et al.[2] hypothesized a passive form of animal-mediated directed dispersal that occurs without specialized plant traits beyond fruit production (hereafter, passive directed dispersal [PDD]). PDD emerges when three conditions are met: (1) animal vectors track resources in heterogenous environments, (2) this behavior results in seed rain skewed toward those resources, and (3) the locations with vector resources are also favorable destinations for the dispersed plants.[2] Despite the prevalence of diffuse dispersal mutualisms and resource tracking, empirical evaluations of PDD remain limited.[2,3]

Fire is a pervasive eco-evolutionary force that shapes plant assemblages,[4,5] yet relatively few studies explore the interaction between endozoochory (i.e., plant dispersal via ingestion by animals) and fire in frequent-fire systems.[6–8] Two factors suggest that endozoochory can generate PDD in ecosystems where fire is common. First, conditions in recently burned areas can advantage plant species with one or more life-history stages adapted to fire and disturbance.[4,9,10] Second, recent burns attract diverse seed-dispersing animals.[11–13] Although originally coined to describe herbivore attraction to recovering forage in recent burns,[14] a more broadly defined "magnet effect" of recent fire may link plants and fire via resource tracking by these animal vectors.

We hypothesized that the magnet effect of wildland fire generates the necessary conditions for PDD in a diffuse mutualism of seed-dispersing birds and early-successional, generalist focal plant taxa promoted by frequent fire. Birds are observed at active fires, immediately following fires, and during vegetation recovery in the year following fire,[11,12,15–18] and their perching behavior provides an opportunity to monitor bird-mediated

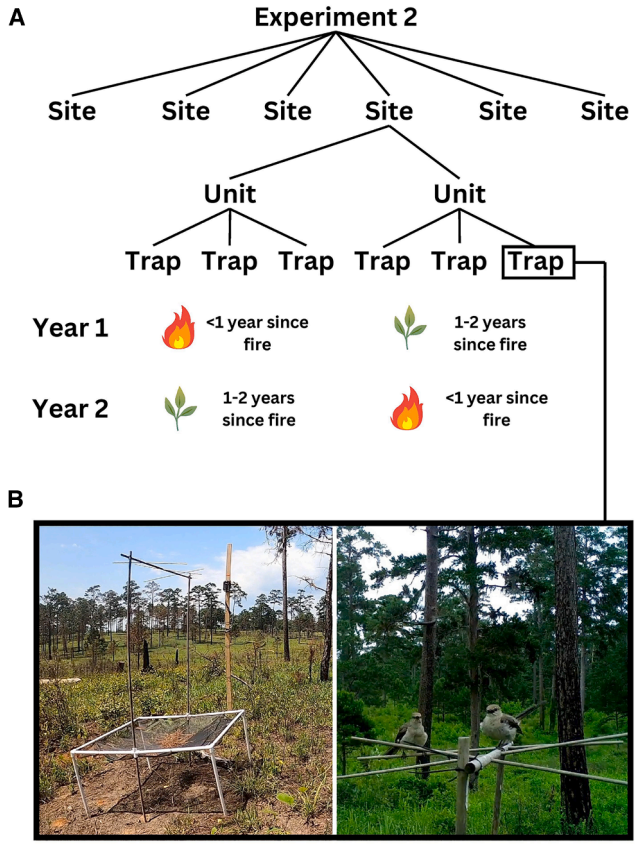

Figure 1. Game cameras monitored artificial perches positioned above seed traps in our paired and nested second experiment

We monitored avian seed dispersal using game cameras and artificial perches positioned above a 1 m^2 seed collection platform (i.e., seed trap). We placed these traps at 6 sites made from 12 paired units. Each unit consisted of 3 seed traps (n = 6 per site, 36 total traps). We monitored each unit in a year following fire and in 1–2 years since fire by swapping treatments after the first year of the experiment.

seed dispersal.[19–21] Post-dispersal recruitment and fitness of our focal plant taxa partly depends on positive feedback between fire frequency and fire-adapted vegetation.[10,22,23] The magnet effect of recent fire on seed-dispersing birds (i.e., in the year following fire) should increase the probability that focal plant taxa establishing from seed banks or seed rain encounter this recurring fire.[24,25] Two predictions arise if birds deliver PDD during the magnet effect in our frequent-fire ecosystem. First, fire should provide a fitness advantage to plants benefiting from PDD. Second, the magnet effect of recent fire should direct bird-dispersed seeds from those plants to favorable, recently burned destinations. We explored these predictions in two distinct, but complementary, experiments designed to evaluate different components of the PDD hypothesis.

Experiment 1: Does frequent fire promote locally common bird-dispersed plants?

The first experiment was a six-decade-long, continuous manipulation of fire frequency in North American upland pine savanna, with biennial fire and fire-exclusion treatments that assessed the net effects of recurring fire on three focal bird-dispersed plant taxa that are frequently dispersed beneath artificial perches: *Callicarpa americana*, *Rhus copallinum*, and *Rubus* spp. PDD predicts that frequently burned destinations preferred by birds in our system provide an advantage to our focal taxa, independent of increased seed arrival.[26,27] This prediction is supported by literature demonstrating that fire can promote establishment and fruit production for these focal taxa and other early-successional and generalist species.[28–31] Accordingly, we expected biennial fire to enhance indicators of resource availability and fecundity in focal taxa compared with fire exclusion (i.e., frequency of occurence along transects and fruit production).[32,33]

Experiment 2: Does the magnet effect increase bird activity and vectored seed rain at artificial perches?

Our second, 2-year field experiment used a paired crossover design to monitor bird activity and seed rain at artificial perches erected above seed traps in areas burned <1 year prior, paired with units burned between 1 and 2 years prior (Figure 1A). Recurring fire can alter bird communities by maintaining open-canopy conditions and a herbaceous understory.[26] We isolated the magnet effect from fire-driven habitat heterogeneity by conducting the second experiment in separate frequent-fire units. After the first year of fire application, we burned the "1- to 2-years-since-fire" units and allowed the vegetation to continue to grow in the "<1-year-since-fire" units. Each treatment in year 1 thus became the opposing treatment in year 2, further isolating the magnet effect from variation in bird activity associated with landscape characteristics other than fire frequency. We also measured four other potentially confounding factors at or beneath the artificial perches: avian defecation rate, natural perch availability, seed loss, and fruit availability. After accounting for these potentially confounding factors, we anticipated greater seed rain <1 year since fire based on comparisons with uncorrected totals from locations burned 1–2 years prior.

RESULTS

Experiment 1: Does frequent fire promote locally common bird-dispersed plants?

In our survey for focal plant taxa, we detected *C. americana* on 10 transects, *R. copallinum* on 17 transects, and *Rubus* spp. on 11 transects (Figure 2). *Rhus copallinum* and *Rubus* spp. only occurred with biennial fire, which prevented statistical analyses. Results from Poisson and binomial generalized linear mixed models (GLMMs) demonstrated that total *C. americana* counts (ratio = 1.1, SE = 0.7, z-ratio = 0.1, p = 0.948) and observation probability (ratio = 0.6, SE = 0.4, z-ratio = 0.7, p = 0.498) remained constant across biennial fire and fire-exclusion plots. The *C. americana* Poisson model explained 1%–9% of the variance in the data, all attributable to the random effect of site (<0.01% explained by fixed effects). The *C. americana* binomial model explained 12%–69% of the data, with 9%–56% attributable to the random effect of site, respectively.

Most of the individual plants detected for fruit surveys occurred with biennial fire (n = 65) compared with fire exclusion (n = 34; Figure 3). *R. copallinum* and *Rubus* spp. only produced fruit with biennial fire, but we detected *R. copallinum* (n = 5) and *Rubus* spp. (n = 5) individuals with no fruit in fire-exclusion plots.

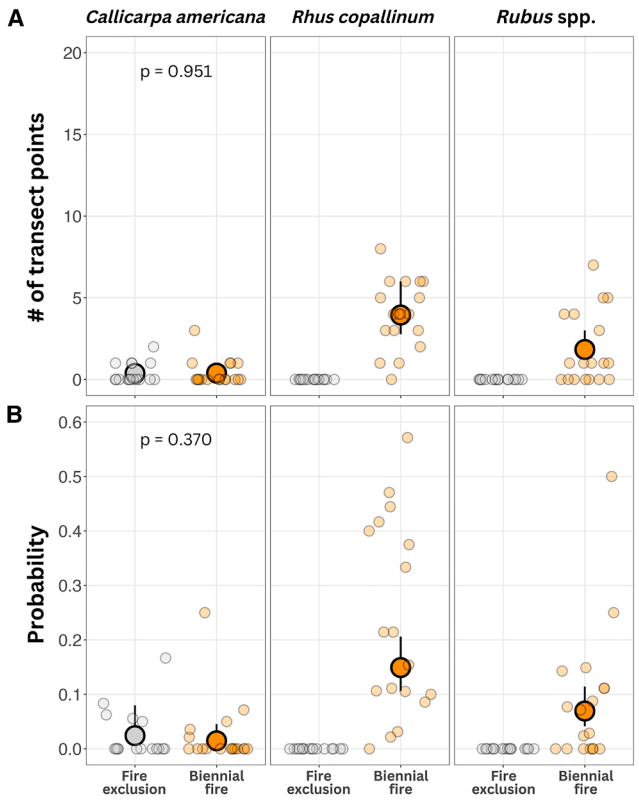

Figure 2. Some focal bird-dispersed plant taxa occur more with frequent fire

Estimated marginal means (solid points) and 95% confidence intervals of observation probability at transect points in fire-exclusion (gray) and 2-year fire-return-interval (orange) plots for *Callicarpa americana*, *Rhus copallinum*, and *Rubus* spp. Translucent points represent values for each transect (n = 16–18). p values derived from general linear mixed effects models comparing the number of transect points with *C. americana* present in fire-exclusion and 2-year-fire-return-interval plots.
See also Table S7.

Results of a reduced generalized linear model (GLM) with a negative binomial distribution demonstrated that fruit production increased by a factor of 16.5 for *C. americana* (SE = 7.7, z-ratio = 6.0) in biennial fire. This model explained 22%–62% of the variance (only fixed effects).

Experiment 2: Does the magnet effect increase bird activity and vectored seed rain at artificial perches?

Avian *observations*

Of the 64 species and taxonomic groupings (i.e., other sparrows, new world thrushes, and *Setophaga* sp. that we could not identify to species) detected with camera monitoring at artificial perches, we identified 43 species and 9 other taxonomic groupings with diets that can include fruit (Table S1). Adjusted estimated marginal means of annual avian observations at artificial perches derived from a GLMM with a negative binomial distribution increased by 30 in <1 year since fire compared with areas burned 1–2 years prior (χ^2 = 6.5, degrees of freedom [df] = 1; Figure 4). For many of the most frequent birds visiting artificial perches, this increase occurred in the growing season immediately following the prescribed fire application in March, but

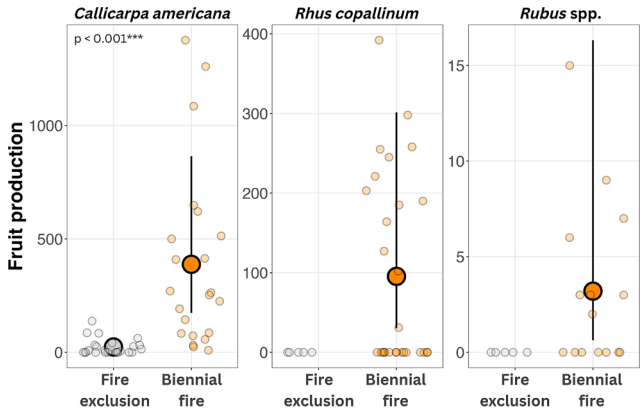

Figure 3. Focal bird-dispersed plant taxa produce more fruit with frequent fire

Estimated marginal means (solid points) and 95% confidence intervals of fruit counts in fire-exclusion (gray) and 2-year fire-return-interval (orange) plots for *Callicarpa americana*, *Rhus copallinum*, and *Rubus* spp. Translucent points represent values for *C. americana* (n = 46), *R. copallinum* (n = 33), and *Rubus* spp. (n = 20) individuals. p values derived from general linear mixed effects models comparing fruits on individual plants in fire-exclusion and 2-year-fire-return-interval plots.

some taxa favored the fall (Figure S1). The effect of fire was stronger in units burned the second year (χ^2 = 12.5, df = 1, p <0.001; Figure 4; Table S2). The model explained 65%–72% of the total variance in the dataset, with 10%–11% attributable to the fixed effects of fire treatment and burn year and the remaining attributable to random effects. Variance associated with site (SD = 0.7; Figure S2) was greater than individual traps nested within units and sites (SD = 0.4) and units nested within sites (SD = 0.3).

Projected seed counts

We collected nearly 12,800 seeds from focal taxa beneath artificial perches across 2 monitoring years. Focal taxa accounted for 72% of the total identified taxa with morphological adaptations encouraging endozoochoric dispersal and 23% of the total seeds collected. Results from a GLMM with a negative binomial distribution provided evidence that raw seed totals obscured the relationship between recent fire and seed arrival of focal bird-dispersed seeds (Table S3). After multiplying by the ratio of fruit availability and then seed loss across treatments (see below), the estimated marginal means of corrected annual seed counts in <1 year since fire increased by a factor of 3.5 for *C. americana*, 2.8 for *R. copallinum*, and 239.2 for *Rubus* spp. compared with those in 1–2 years since fire (Figures 5 and S3). The model accounted for 43%–82% of the variance in the data, with 28%–54% of this attributable to the fixed effects of fire treatment, focal taxa, and burn year. Variance associated with site (SD = 1.2; Figure S4) was greater than that associated with individual traps nested within sites (SD = 0.6).

Examining potential confounding factors in experiment 2

Avian defecation observations Results from a binomial GLMM demonstrated that the mean probability of recording defecation events during any individual bird observation at an artificial perch

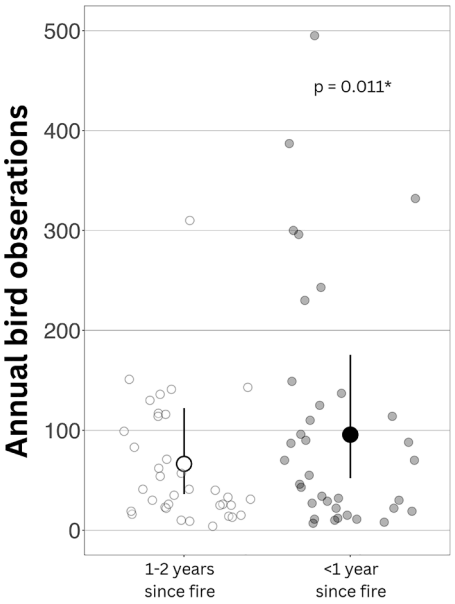

Figure 4. Recent fire (<1 year) increased bird observation at artificial perches

Estimated marginal means and confidence limits for annual bird observations from game cameras at 36 artificial perches in 1–2 years (empty) and <1 year since fire (solid). *p* values derived from general linear mixed effects model comparing total seed-dispersing bird observations in the year following fire to 1–2 years since fire.

See also Figures S1 and S2; Tables S1 and S2.

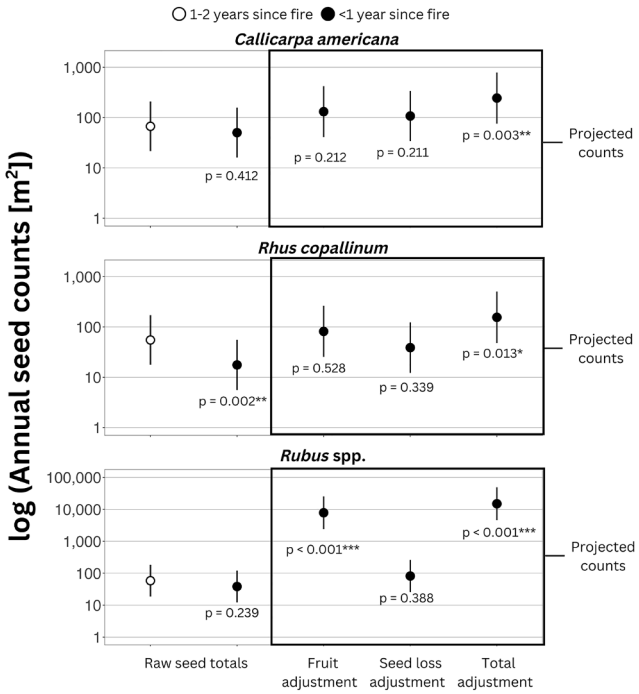

Figure 5. Recent fire (<1 year) increased seeds from focal plant taxa arriving beneath artificial perches after adjusting for fruit availability and seed loss

Estimated marginal means and confidence limits for natural logarithm-transformed annual seed counts at 36 traps beneath artificial perches in 1–2 years (empty) and <1 year since fire (solid) for *Callicarpa americana*, *Rhus copallinum*, and *Rubus* spp. Annual seed counts in <1-year-since-fire units are adjusted by multiplying raw values by ratios of fruit observation and seed loss probability. These ratios account for the increased fruit availability in 1–2 years since fire and increased seed loss in <1 year since fire. *p* values derived from general linear mixed effects models comparing seed counts and projected seed counts in the year following fire with 1–2 years since fire.

See also Figures S3 and S4; Tables S3–S5.

($\widehat{p}_{model}$ = 0.05, 95% confidence interval [CI] [0.04, 0.06]) remained constant across <1-year-since-fire areas and areas burned 1–2 years prior (χ^2 = 2.1, df = 1, p = 0.147; Figure 6A) and year of fire application (χ^2 = 1.1, df = 1, p = 0.287), and no interaction occurred (χ^2 = 0.0, df = 1, p = 0.979). This model explained 0%–2% of the variance in the data, with 0%–1% attributable to the random effects of site and individual traps. Variance attributable to the random effect of individual trap nested within site (SD = 0.2) was greater than that of site (SD = 0.1).

Lower-midstory perch availability and quality Results from a GLMM with a Gaussian distribution indicated that the model-estimated mean distance of 3.1 m to nearest lower midstory (95% CI [2.4, 4.1]) remained constant across fire treatments (χ^2 = 0.5, df = 1, p = 0.494; Figure 6B). This model explained 6% of the variance in the data, with <0.01% attributable to fixed effects. Variance attributable to the random effect of trap nested within site (variance = 0.07, SD = 0.27) was greater than that of site (variance = 0.06, SD = 0.25).

The model-estimated probabilities of the lower-midstory perch having foliage in <1 year since fire (mean = 0.7, 95% CI [0.6, 0.9]) and 1–2 years since fire (mean = 0.6, 95% CI [0.5, 0.7]) did not significantly differ (χ^2 = 2.0, df = 1, p = 0.160). This model explained 2%–3% of the data, with < 0.01% attributable to the random effect of site.

Calculating fruit availability Results from a binomial GLMM revealed that recent fire (<1 year) decreased fruit availability, but this effect varied across species (χ^2 = 15.1, df = 2, p < 0.001). Overall, the probability of fruit detection was highest for *R. copallinum* (mean = 0.04, 95% CI [0.02, 0.06]), followed by *C. americana* (mean = 0.02, 95% CI [0.01, 0.03]) and *Rubus* spp. (mean = 0.01, 95% CI [0.00, 0.02]). These overall probabilities were driven by recent fire, which decreased the odds of fruit detection by a factor of 0.4 for *C. americana* (SE = 0.17, p = 0.034), 0.3 for *R. copallinum* (SE = 0.12, p = 0.005), and 0.01 for *Rubus* spp. (SE = 0.01, p < 0.001; Table S4). The odds of detecting fruit were higher in 1–2 years since fire than in <1 year since fire at every site, and we only detected *Rubus* spp. fruit once in <1 year since fire (Table S4). The model explained 23%–62% of the variation in the data, of which 7%–20% was attributable to the random effects of the overdispersion term (SD = 1.2), unit nested within site (SD = 0.4), and site (SD = 0.3).Seed loss probability Results from a binomial GLMM revealed that recent fire (<1 year) increased the average odds of seed loss by a factor of 3.8 (SE = 1.8) compared with 1–2 years since fire (p = 0.006; Figure 7A). Seed loss was greater in <1 year since fire in 4 out of 6 sites and in 5 of 6 sequential trials occurring in the year following fire (Table S5). Species varied in the probability of being lost (χ^2 = 6.4, df = 2, p = 0.040; Figures 7B and 7C), and the odds of losing a seed from the trap increased by approximately 9% (SE = 0.03) for each additional day of trial duration. The

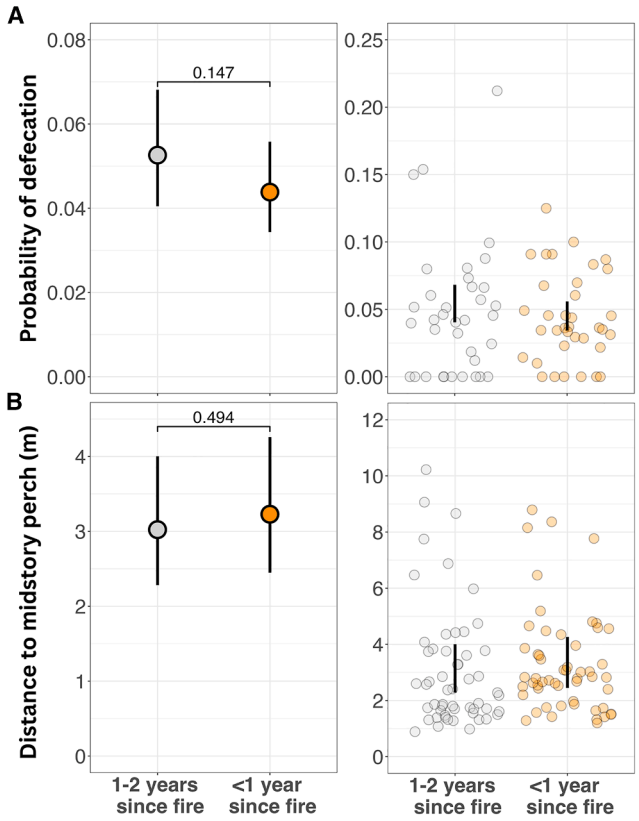

Figure 6. Probability of observing avian defecation at artificial perches and lower-midstory perch availability is similar in <1 and 1–2 years after fire

(A) Left graph depicts estimated marginal means of the probability of observing defecation events and confidence limits (solid lines) for 1–2 years (gray) and <1 year (orange) since fire. Right graph shows probability for individual traps in treatment years (n = 72) with confidence limits (black line).

(B) Left graph depicts observed mean distance to nearest three lower-midstory perches at each trap for 1–2 years (gray) and <1 year (orange) since fire with confidence limits. Right graph shows individual values for distance to nearest lower-midstory perch (each trap represented three times) with confidence limits (n = 108).

p values derived from general linear mixed effects models comparing the probability of observing avian defecation events and distance to nearest midstory perch in the year following fire to 1–2 years since fire.

model explained 65%–69% of the variance in the data, of which 51%–54% was attributable to the random effects of the overdispersion term (SD = 2.0), trap nested within site (SD = 1.3), and site (SD = 0.3).

DISCUSSION

Our first experiment confirmed that more than 60 years of biennial fire promotes widespread and locally common bird-dispersed focal plant taxa known to thrive with frequent fire. Our second experiment revealed that recent fire attracts the birds dispersing those plants to artificial perches in the year following fire. Based on projections, *Rubus* spp. seeds arrived more often in <1 year compared with 1–2 years since fire, after adjusting only for fruit availability, indicating that the magnet effect compensated for increased seed loss. However, after jointly

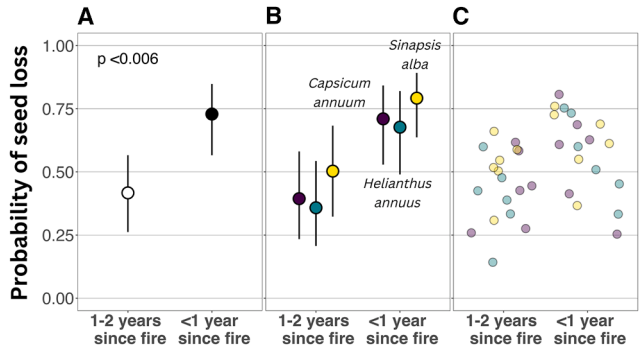

Figure 7. Fire increased seed loss from seed traps beneath artificial perches

(A) Estimated marginal means of seed loss probability and confidence limits (solid lines) for 1–2 years (hollow) and <1 year (filled) since fire, averaged over trials (mean length = 14 days). Each of the six seed loss trials consisted of seeds from three plant species (i.e., *Capsicum annuum*, *Sinapis alba*, and *Helianthus annuus*).

(B) Estimated marginal mean probability and confidence limits (solid lines) for *C. annuum* (purple), *H. annuus* (green), and *S. alba* (yellow) in 1–2 years and <1 year since fire.

(C) Mean probability of seed loss for species at individual traps (n = 36) averaged over six trials that varied in length from 6–23 days.

p values derived from general linear mixed effects models comparing seed loss in the year following fire to 1–2 years since fire.

adjusting for seed loss and fruit availability, the magnet effect of recent fire attracted seeds of all focal taxa beyond what may be expected in conditions similar to 1–2 years since fire. This flow of seeds toward <1 year since fire increases the probability that plants encounter the recurring fire that maintains favorable open-canopy conditions and ecosystem flammability.[22,23] Accordingly, our data demonstrate that wildland fire presents the necessary conditions for PDD.

The effect of recurring fire on focal bird-dispersed taxa

One shade-tolerant focal taxa (*C. americana*) occurred in biennial fire and fire-exclusion plots, but other focal taxa (*R. copallinum* and *Rubus* spp.) were nearly completely limited to gaps and edges after 60+ years of fire exclusion. This pattern generally confirms the reported life-history traits of focal taxa and suggests that recurring fire promotes recruitment for some taxa.[34–37] Alternatively, these patterns could also result from seed limitation (i.e., more individuals would establish with greater seed arrival).[37] However, given the potential for vector overlap in diffuse mutualisms and the presence of *C. americana* in biennial fire and fire-exclusion plots, it is plausible that seeds from the other focal taxa also arrived in both treatments.

Despite differences in how often they were encountered across treatments, all focal taxa produced more fruit with biennial fire, indicating that recurring fire promotes plant performance.[32,33] The conditions that promote fruit production also encourage fruit removal,[28] leading to more effective seed dispersal. Collectively, these findings are supported by previous literature reporting positive responses of these and other generalist and early-successional plant species to decreased competition and increased resource availability.[28–31]

The magnet effect of recent fire on avian vectors

The magnet effect of recent fire conventionally describes the response of vertebrate herbivores to the pulse of high-quality forage in recent burns.[14,38–40] Fruit availability often drives avian resource tracking,[3] but ripe fruit in <1 year since fire was nearly absent in our surveys and similar works.[41–43] Instead, avian vectors may be attracted to our artificial perches in <1 year since fire by changes in vegetation structure,[44,45] other food resources (e.g., quality and accessibility),[12,46,47] territory availability,[48] and exploratory behavior (i.e., neophilia *sensu* Greenberg[49]). For example, insectivores in our experiment visited more often in the months after the fire, as insects recolonized. In contrast, resident omnivores that utilize diverse resources responded throughout the growing season. Our results highlight the utility of the magnet effect for understanding additional fire-driven community interactions beyond pyric-herbivory.

Seed arrival resulting from the magnet effect

Raw seed arrival values were comparable or lower in <1 year since fire, despite elevated bird activity at artificial perches. This discrepancy likely resulted, in part, from decreased fruit availability after recent fire, which increased the distance that birds traveled to reach artificial perches after fruit consumption.[50] Consequently, birds likely deposited seeds before reaching artificial perches more often in <1 year than in 1–2 years since fire. Nevertheless, by increasing avian activity at artificial perches, the magnet effect of recent fire distributed seed rain across our frequent-fire landscape by directing seeds from 1–2 years since fire toward <1 year since fire.

Recent fire also increased loss from seed traps between collections, potentially due to elevated wind speeds associated with changes in understory vegetation or increased seed removal by animals. One potential explanation of seed removal by animals is seed predation. Accordingly, higher seed predation could negate the fitness benefit of dispersal toward <1 year since fire. However, seed removal from seed traps by animals may not accurately represent seed predation. Seeds may be easier to detect on the seed trap collection surface than on exposed mineral soil in recent burns. Moreover, seed removal from traps by animals can also indicate secondary seed dispersal, with potentially positive outcomes for plant establishment.[51,52] Even if seed predation occurs more often in <1 year since fire, PDD is possible if the beneficial conditions associated with fire result in greater fitness overall compared with random dispersal.

Our projections of seed rain that incorporate adjustments for seed removal and fruit availability are inexact representations of seed arrival beneath perches. Using commercial seeds likely affected estimates of seed loss, and our single metric for seed loss obscured variation across species. Similarly, our adjustments assumed a simple relationship between fruit availability and seed dispersal by birds. This approach disregarded the possibility of non-monotonic relationships between distance and dispersal probability,[50] including those potentially resulting from central foraging[53] and rare-biased seed dispersal.[21] Although these caveats highlight limitations in our approach, our projections more effectively demonstrate the magnet effect of recent fire on bird-mediated seed dispersal than raw seed totals that omit the confounding effects of fruit availability and seed loss associated with recent fire.

Potential community effects of PDD after fire

Seed dispersal by animals toward frequently burned areas is one among a suite of plant, consumer, and abiotic interactions mediated by fire.[39,54–60] Indeed, plants have a suite of fire-adapted traits that may drive community assembly (e.g., resprouting and seed banking).[5] At a minimum, our results indicate that seed dispersal by animals influences community assembly and trophic interactions in pyric ecosystems by increasing the probability that seeds arrive at recent burns. We highlight the potential positive outcomes of these dispersal patterns for some regionally widespread and locally common bird-dispersed taxa promoted by fire, but many early-successional and generalist plants will similarly benefit, while other plant taxa respond negatively or neutrally. In either case, post-fire seed dispersal and seed fate for these plant taxa likely depends on variation within mutualisms and ecosystems across space, time, and fire characteristics.[42,43,61–63] For example, the landscape for experiment two provided birds with ample opportunities to travel back and forth among evenly dispersed <1-year-since-fire and 1- to 2-years-since-fire areas, which likely influenced the patterns in bird activity and seed rain that we observed.[64] More broadly, seed dispersal by animals after recent fire will also vary across ecosystems due to differences in abiotic conditions, fire regimes, and plant and animal traits.[8,12,65,66]

Our biennial fire treatment in old fields is a reasonable choice of study system, given regional initiatives to restore pine savannas in post-agricultural areas with frequent fire.[67,68] In this interconnected system, avian vectors that subsist on old-field, fire-maintained vegetation disperse those same plant species while seeking out recently burned areas. This process likely promotes homogeneity across vegetation communities in our landscape, but in other circumstances it could also facilitate the spread of introduced species,[69] mediate mesophication,[22,23,70] or drive forest recovery and expansion.[19,20,71] Despite this, research exploring plant-animal-fire interactions in the context of land management often focuses on pyric-herbivory.[72,73] We propose integrating seed dispersal by birds into a broader understanding—including pollination, herbivory, seed predation, and other forms of animal-mediated seed dispersal (e.g., myrmecochory and scatter-hoarding—to further management, restoration, and conservation efforts in frequent-fire ecosystems.[39,51,52,54,55,57,60]

Moving forward

Our sampling design underrepresents spatiotemporal, interspecific, and intraspecific variation in plant performance, avian activity, seed arrival, and fire regimes. For example, *Rubus* spp., which fruited relatively soon after prescribed fire, responded more strongly to recent fire than other focal taxa that fruited 3–4 months later, indicating potential phenological considerations. Similarly, differences in bird-mediated seed dispersal that we demonstrated across areas differing by only a year in time since fire likely vary with longer temporal comparisons. Moreover, the secondary movement and fate of individual propagules, the role of microsite characteristics, and the effects of seed rain density on post-fire destination quality remain areas for future investigation.[74,75] Finally, although we focused on seed dispersal after fire by a suite of birds visiting artificial

perches that mimic the lower midstory, other forest strata remain unmeasured. Future research should deconstruct the complexity of PDD after fire while assessing the biological relevance and generalizability of our findings across fire regimes, taxa, and ecosystems.

Conclusion

Our evidence suggests that the necessary conditions for PDD occur in a diffuse, bird-mediated seed dispersal mutualism with frequent fire in pine savannas. Considering that much of the terrestrial planet is flammable, seed dispersal by birds toward recent burns provides additional evidence that directed dispersal may occur more often than previously expected.[1,2,4] More broadly, the mechanisms underlying PDD after wildland fire occur in other contexts where resource tracking occurs at locations that favor animal-dispersed plants.[1–3]

RESOURCE AVAILABILITY

Lead contact

Direct requests for further information to the lead contact, David S. Mason (david.mason@jonesctr.org).

Materials availability

All the data collected and used for analysis in this study are available for download at www.datadryad.org (DOI: 10.5061/dryad.tqjq2bw77).

Data and code availability

- Data have been deposited at Dryad and are publicly available as of the date of publication at 10.5061/dryad.tqjq2bw77.
- All original code has been deposited at GitHub and is publicly available at https://github.com/masond-UF/Fire-promotes-PDD-by-birds as of the date of publication.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization: D.S.M., K.M.R., P.G.H., E.M.B., J.L.W., and M.A.L; investigation: D.S.M. and M.A.L.; methodology: D.S.M., P.G.H., and M.A.L.; project administration: D.S.M., K.M.R., and M.A.L.; resources: K.M.R. and M.A.L.; supervision: K.M.R., P.G.H., E.M.B., J.L.W., and M.A.L.; visualization: D.S.M.; writing – original draft: D.S.M.; writing – review & editing: D.S.M., K.M.R., P.G.H., E.M.B., J.L.W., and M.A.L.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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REFERENCES

1. Wenny, D.G. (2001). Advantages of seed dispersal: a re-evaluation of directed dispersal. Evol. Ecol. Res. *3*, 37–50.
2. Mason, D.S., Baruzzi, C., and Lashley, M.A. (2022). Passive directed dispersal of plants by animals. Biol. Rev. Camb. Philos. Soc. *97*, 1908–1929. https://doi.org/10.1111/brv.12875.
3. Gleditsch, J.M., Hruska, A.M., and Foster, J.T. (2017). Connecting resource tracking by frugivores to temporal variation in seed dispersal networks. Front. Ecol. Evol. *5*, 98. https://doi.org/10.3389/fevo.2017.00098.
4. Bond, W.J., and Keeley, J.E. (2005). Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. *20*, 387–394. https://doi.org/10.1016/j.tree.2005.04.025.
5. Keeley, J.E., and Pausas, J.G. (2022). Evolutionary ecology of fire. Annu. Rev. Ecol. Evol. Syst. *53*, 203–225. https://doi.org/10.1146/annurev-ecolsys-102320-095612.
6. Peguero, G., and Espelta, J.M. (2014). Endozoochory and fire as germination triggers in neotropical dry forests: an experimental test. Biotropica *46*, 83–89. https://doi.org/10.1111/btp.12076.
7. Lado, T.F., Jibi, W.F., and Moilinga, P.T. (2018). Species-specific germination responses to fire-associated heat of elephant-dispersed seeds in Nimule National Park, South Sudan. Biotropica *50*, 483–486. https://doi.org/10.1111/btp.12554.
8. Keeley, J.E., and Fotheringham, C.J. (2000). Role of fire in regeneration from seed. In Seeds: the Ecology of Regeneration in Plant Communities, M. Fenner, ed. (CABI Publishing International), pp. 311–330. https://doi.org/10.1079/9780851994321.0311.
9. Pilon, N.A.L., Cava, M.G.B., Hoffmann, W.A., Abreu, R.C.R., Fidelis, A., and Durigan, G. (2021). The diversity of post-fire regeneration strategies in the cerrado ground layer. J. Ecol. *109*, 154–166. https://doi.org/10.1111/1365-2745.13456.

10. Robertson, K.M., Hermann, S.M., and Staller, E.L. (2021). Frequent prescribed fire sustains old field Loblolly Pine–Shortleaf Pine Woodland Communities: Results of a 53-year study. J. For. *119*, 549–556. https://doi.org/10.1093/jofore/fvab035.

11. Komarek, E.V. (1969). Fire and animal behavior. In Proceedings of the 9th Tall Timbers Fire Ecology Conference, E.V. Komarek, ed. (Tall Timbers Research Station), pp. 160–207.

12. Frost, P.G.H. (1984). The responses and survival of organisms in fire-prone environments. In Ecological Effects of Fire in South African Ecosystems, P.V. de Booysen, and N.M. Tainton, eds. (Springer Berlin Heidelberg), pp. 273–309. https://doi.org/10.1007/978-3-642-69805-7_13.

13. Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., and Stambaugh, M.C. (2016). Fire effects on wildlife in the Central Hardwoods and Appalachian regions, USA. Fire Ecol. *12*, 127–159. https://doi.org/10.4996/fireecology.1202127.

14. Archibald, S., Bond, W.J., Stock, W.D., and Fairbanks, D.H.K. (2005). Shaping the landscape: fire–grazer interactions in an African savanna. Ecol. Appl. *15*, 96–109. https://doi.org/10.1890/03-5210.

15. Edwards, W.R., and Ellis, J.A. (1969). Responses of three avian species to burning. Wilson Bull. *81*, 338–339.

16. Emlen, J.T. (1970). Habitat selection by birds following a forest fire. Ecology *51*, 343–345. https://doi.org/10.2307/1933677.

17. Vogl, R.J. (1973). Effects of fire on the plants and animals of a Florida wetland. Am. Midl. Nat. *89*, 334–347. https://doi.org/10.2307/2424038.

18. Lowe, P.O., Ffolliott, P.F., Dieterich, J.H., and Patton, D.R. (1978). Determining potential wildlife benefits from wildfire in Arizona ponderosa pine forests. Gen. Tech. Rep., RM-52 (United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station).

19. McClanahan, T.R., and Wolfe, R.W. (1993). Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conserv. Biol. *7*, 279–288. https://doi.org/10.1046/j.1523-1739.1993.07020279.x.

20. Cavallero, L., Raffaele, E., and Aizen, M.A. (2013). Birds as mediators of passive restoration during early post-fire recovery. Biol. Conserv. *158*, 342–350. https://doi.org/10.1016/j.biocon.2012.10.004.

21. Carlo, T.A., and Morales, J.M. (2016). Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. Ecology *97*, 1819–1831. https://doi.org/10.1890/15-2147.1.

22. Nowacki, G.J., and Abrams, M.D. (2008). The demise of fire and "mesophication" of forests in the eastern United States. BioScience *58*, 123–138. https://doi.org/10.1641/B580207.

23. Hanberry, B.B. (2021). Transition from fire-dependent open forests: Alternative ecosystem states in the southeastern United States. Diversity *13*, 411. https://doi.org/10.3390/d13090411.

24. Cain, M.D., and Shelton, M.G. (2003). Fire effects on germination of seeds from *Rhus* and *Rubus*: competitors to pine during natural regeneration. New For. *26*, 51–64. https://doi.org/10.1023/A:1024406209842.

25. Diaz-Toribio, M.H., and Putz, F.E. (2017). Clear-cuts are not clean slates: residual vegetation impediments to savanna restoration. Castanea *82*, 58–68. https://doi.org/10.2179/16-099.

26. Engstrom, R.T., Vickery, P.D., Perkins, D.W., and Shriver, W.G. (2005). Effects of fire regime on birds in southeastern pine savannas and native prairies. Stud. Avian Biol. *30*, 147–160.

27. Steen, D.A., Conner, L.M., Smith, L.L., Provencher, L., Hiers, J.K., Pokswinski, S., Helms, B.S., and Guyer, C. (2013). Bird assemblage response to restoration of fire-suppressed longleaf pine sandhills. Ecol. Appl. *23*, 134–147. https://doi.org/10.1890/12-0197.1.

28. Thompson, J.N., and Willson, M.F. (1978). Disturbance and the dispersal of fleshy fruits. Science *200*, 1161–1163. https://doi.org/10.1126/science.200.4346.1161.

29. Zwolinski, M.J. (1990). Fire effects on vegetation and succession. In Proceedings of the a symposium Effects of fire management of Southwestern Natural Resources, M.J. Krammes, tech. coord. (Gen. Tech. Rep. RM-191, US Department of Agriculture, Forest Service, Rocky Mountain Forest, and Range Experiment Station), pp. 18–24.

30. Ostertag, T.E., and Robertson, K.M. (2007). A comparison of native versus old-field vegetation in upland pinelands managed with frequent fire, South Georgia, USA. In Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems, R.E. Masters and K.E.M. Galley, eds. (Tall Timbers Research Station), pp. 109–120.

31. Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., and Swanson, F.J. (2010). The forgotten stage of forest succession: early-successional ecosystems on forest sites. Front. Ecol. Environ. *9*, 117–125. https://doi.org/10.1890/090157.

32. Stephenson, A.G. (1981). Flower and fruit abortion: proximate causes and ultimate functions. Annu. Rev. Ecol. Syst. *12*, 253–279. https://doi.org/10.1146/annurev.es.12.110181.001345.

33. Younginger, B.S., Sirová, D., Cruzan, M.B., and Ballhorn, D.J. (2017). Is biomass a reliable estimate of plant fitness? Appl. Plant Sci. *5*, apps.1600094. https://doi.org/10.3732/apps.1600094.

34. Coladonato, M. (1992). Callicarpa americana. Fire Effects Information System (United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory [Producer])).

35. Coladonato, M. (1992). Rhus copallinum. Fire Effects Information System (United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory [Producer]).

36. Glitzenstein, J.S., Streng, D.R., Masters, R.E., Robertson, K.M., and Hermann, S.M. (2012). Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. For. Ecol. Manag. *264*, 197–209. https://doi.org/10.1016/j.foreco.2011.10.014.

37. Beckman, N.G., and Sullivan, L.L. (2023). The causes and consequences of seed dispersal. Annu. Rev. Ecol. Evol. Syst. *54*, 403–427. https://doi.org/10.1146/annurev-ecolsys-102320-104739.

38. Cherry, M.J., Chandler, R.B., Garrison, E.P., Crawford, D.A., Kelly, B.D., Shindle, D.B., Godsea, K.G., Miller, K.V., and Conner, L.M. (2018). Wildfire affects space use and movement of white-tailed deer in a tropical pyric landscape. For. Ecol. Manag. *409*, 161–169. https://doi.org/10.1016/j.foreco.2017.11.007.

39. Westlake, S.M., Mason, D., Lázaro-Lobo, A., Burr, P., McCollum, J.R., Chance, D., and Lashley, M.A. (2020). The magnet effect of fire on herbivores affects plant community structure in a forested system. For. Ecol. Manag. *458*, 117794. https://doi.org/10.1016/j.foreco.2019.117794.

40. Thapa, S.K., de Jong, J.F., Hof, A.R., Subedi, N., Joshi, L.R., and Prins, H.H.T. (2022). Fire and forage quality: Postfire regrowth quality and pyric herbivory in subtropical grasslands of Nepal. Ecol. Evol. *12*, e8794. https://doi.org/10.1002/ece3.8794.

41. Landers, J.L. (1987). Prescribed burning for managing wildlife in southeastern pine forests. In Proceedings of the Managing Southern Forests for Wildlife and Fish, J.G. Dickson and O.E. Maughn, eds. (Gen. Tech. Rep., SF-50–65 (United States Department of Agriculture, Forest Service)).

42. Lashley, M.A., Chitwood, M.C., DePerno, C.S., and Moorman, C.E. (2017). Frequent fires eliminate fleshy fruit production. For. Ecol. Manag. *405*, 9–12. https://doi.org/10.1016/j.foreco.2017.09.034.

43. Lashley, M.A., Chitwood, M.C., Harper, C.A., DePerno, C.S., and Moorman, C.E. (2015). Variability in fire prescriptions to promote wildlife foods in the longleaf pine ecosystem. Fire Ecol. *11*, 62–79. https://doi.org/10.4996/fireecology.1103062.

44. Addington, R.N., Greene, T.A., Harrison, W.C., Sorrell, G.G., Elmore, M.L., and Hermann, S.M. (2015). Restoring longleaf pine: effects of seasonal prescribed fire and overstory density on vegetation structure of a young longleaf pine plantation. For. Sci. *61*, 135–143. https://doi.org/10.5849/forsci.13-618.

45. Rainsford, F.W., Kelly, L.T., Leonard, S.W.J., and Bennett, A.F. (2021). How does prescribed fire shape bird and plant communities in a temperate

dry forest ecosystem? Ecol. Appl. *31*, e02308. https://doi.org/10.1002/eap.2308.

46. Swengel, A.B. (2001). A literature review of insect responses to fire, compared to other conservation managements of open habitat. Biodivers. Conserv. *10*, 1141–1169. https://doi.org/10.1023/A:1016683807033.
47. Stillman, A.N., Lorenz, T.J., Siegel, R.B., Wilkerson, R.L., Johnson, M., and Tingley, M.W. (2022). Conditional natal dispersal provides a mechanism for populations tracking resource pulses after fire. Behav. Ecol. *33*, 27–36. https://doi.org/10.1093/beheco/arab106.
48. Winter, M. (1999). Relationship of fire history to territory size, breeding density, and habitat of Baird's Sparrow in North Dakota. Stud. Avian Biol. *19*, 171–177.
49. Greenberg, R.S. (2003). The role of neophobia and neophilia in the development of innovative behaviour of birds. In Animal Innovation, S.M. Reader, and K.N. Laland, eds. (Oxford University Press), pp. 175–196. https://doi.org/10.1093/acprof:oso/9780198526223.003.0008.
50. Bullock, J.M., Mallada González, L., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M., and Hooftman, D.A.P. (2017). A synthesis of empirical plant dispersal kernels. J. Ecol. *105*, 6–19. https://doi.org/10.1111/1365-2745.12666.
51. Vander Wall, S.B., Kuhn, K.M., and Beck, M.J. (2005). Seed removal, seed predation, and secondary dispersal. Ecology *86*, 801–806. https://doi.org/10.1890/04-0847.
52. Rogers, H.S., Beckman, N.G., Hartig, F., Johnson, J.S., Pufal, G., Shea, K., Zurell, D., Bullock, J.M., Cantrell, R.S., Loiselle, B., et al. (2019). The total dispersal kernel: a review and future directions. AoB Plants *11*, plz042. https://doi.org/10.1093/aobpla/plz042.
53. Blendinger, P.G., Jiménez, J., Macchi, L., Martín, E., Sánchez, M.S., and Ayup, M.M. (2015). Scale-dependent spatial match between fruits and fruit-eating birds during the breeding season in Yungas Andean forests. Biotropica *47*, 702–711. https://doi.org/10.1111/btp.12247.
54. Parr, C.L., Andersen, A.N., Chastagnol, C., and Duffaud, C. (2007). Savanna fires increase rates and distances of seed dispersal by ants. Oecologia *151*, 33–41. https://doi.org/10.1007/s00442-006-0570-5.
55. Zwolak, R., Pearson, D.E., Ortega, Y.K., and Crone, E.E. (2010). Fire and mice: Seed predation moderates fire's influence on conifer recruitment. Ecology *91*, 1124–1131. https://doi.org/10.1890/09-0332.1.
56. Myers, J.A., and Harms, K.E. (2011). Seed arrival and ecological filters interact to assemble high-diversity plant communities. Ecology *92*, 676–686. https://doi.org/10.1890/10-1001.1.
57. Willis, J.L., Schnake, D.K., DePerno, C.S., Lashley, M.A., Wetzstein, B., and Yow, J. (2021). Tree encroachment impacts on seed predator selection and seedling establishment in degraded pine woodlands. Appl. Veg. Sci. *24*, e12570. https://doi.org/10.1111/avsc.12570.
58. Foster, C.N., Banks, S.C., Cary, G.J., Johnson, C.N., Lindenmayer, D.B., and Valentine, L.E. (2020). Animals as agents in fire regimes. Trends Ecol. Evol. *35*, 346–356. https://doi.org/10.1016/j.tree.2020.01.002.
59. Jorge, M.H., Conner, L.M., Garrison, E.P., and Cherry, M.J. (2022). Avian species richness in a frequently burned ecosystem: a link between pyrodiversity and biodiversity. Landsc. Ecol. *37*, 983–996. https://doi.org/10.1007/s10980-022-01399-8.
60. Carbone, L.M., Tavella, J., Marquez, V., Ashworth, L., Pausas, J.G., and Aguilar, R. (2025). Fire effects on pollination and plant reproduction: a quantitative review. Ann. Bot. *135*, 43–56. https://doi.org/10.1093/aob/mcae033.
61. Barton, P.S., Ikin, K., Smith, A.L., MacGregor, C., and Lindenmayer, D.B. (2014). Vegetation structure moderates the effect of fire on bird assemblages in a heterogeneous landscape. Landsc. Ecol. *29*, 703–714. https://doi.org/10.1007/s10980-014-0017-z.
62. Darracq, A.K., Boone, W.W., and McCleery, R.A. (2016). Burn regime matters: a review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. For. Ecol. Manag. *378*, 214–221. https://doi.org/10.1016/j.foreco.2016.07.039.
63. Mason, D.S., and Lashley, M.A. (2021). Spatial scale in prescribed fire regimes: an understudied aspect in conservation with examples from the southeastern United States. Fire Ecol. *17*, 1–14.
64. Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., and Smith, A.L. (2013). Conceptual domain of the matrix in fragmented landscapes. Trends Ecol. Evol. *28*, 605–613. https://doi.org/10.1016/j.tree.2013.06.010.
65. Fontaine, J.B., and Kennedy, P.L. (2012). Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in US fire-prone forests. Ecol. Appl. *22*, 1547–1561. https://doi.org/10.1890/12-0009.1.
66. Whelan, R.J. (1986). Seed dispersal in relation to fire. In Seed Dispersal, D.R. Murray, ed. (Academic Press), pp. 237–271. https://doi.org/10.1016/B978-0-12-511900-9.50011-5.
67. Brockway, D.G., Outcalt, K.W., Tomczak, D.J., and Johnson, E.E. (2005). Restoration of Longleaf Pine Ecosystems (United States Department of Agriculture, Forest Service, Southern Research Station).
68. Matthews, J.M., Hinchee, J., and Guldin, J.M. (2020). Restoration of Longleaf Pine in the Southern Region of the US Forest Service: an Overview of the Million-Acre Challenge. e–Gen (United States Department of Agriculture, Forest Service, Southern Research Station), pp. 112–119.
69. Vanderhoff, E.N., and Rentsch, J.D. (2022). A Review of Avian Dispersal of Non-Native and Invasive Plants in the Southeastern United States. Castanea *86*, 225–244. https://doi.org/10.2179/0008-7475.86.2.225.
70. Alexander, H.D., Siegert, C., Brewer, J.S., Kreye, J., Lashley, M.A., McDaniel, J.K., Paulson, A.K., Renninger, H.J., and Varner, J.M. (2021). Mesophication of oak landscapes: Evidence, knowledge gaps, and future research. BioScience *71*, 531–542. https://doi.org/10.1093/biosci/biaa169.
71. McDonnell, M.J., and Stiles, E.W. (1983). The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia *56*, 109–116. https://doi.org/10.1007/BF00378225.
72. Fuhlendorf, S.D., and Engle, D.M. (2004). Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. J. Appl. Ecol. *41*, 604–614. https://doi.org/10.1111/j.0021-8901.2004.00937.x.
73. Adhikari, S., Joshi, O., Sorice, M.G., and Fuhlendorf, S.D. (2023). Factors affecting the adoption of patch-burn grazing in the southern Great Plains in the US. Land Use Policy *125*, 106458. https://doi.org/10.1016/j.landusepol.2022.106458.
74. Godínez-Alvarez, H., and Jordano, P. (2007). An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. In Seed Dispersal: Theory and Its Application in a Changing World, A.J. Dennis, E.W. Schupp, R.J. Green, and D.A. Westcott, eds. (CABI Publishing International), pp. 391–406. https://doi.org/10.1079/9781845931650.0391.
75. Spiegel, O., and Nathan, R. (2012). Empirical evaluation of directed dispersal and density-dependent effects across successive recruitment phases. J. Ecol. *100*, 392–404. https://doi.org/10.1111/j.1365-2745.2011.01886.x.
76. R Core Team (2024). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing).
77. 2023). Posit team. R.Studio: Integr. Dev. Environ. R. (Posit Software, PBC).
78. Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., et al. (2019). Welcome to the tidyverse. J. Open Source Softw. *4*, 1686. https://doi.org/10.21105/joss.01686.
79. Delignette-Muller, M.L., and Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. J. Stat. Softw. *64*, 1–34.
80. Hartig, F. (2021). Dharma: Residual Diagnostics for Hierarchical (Multi-level / Mixed) Regression Models (R Package Version 0.3.4).
81. Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P., and Makowski, D. (2021). performance: An R package for assessment, comparison and

testing of statistical models. J. Open Source Softw. *6*, 3139. https://doi.org/10.21105/joss.03139.

82. Lenth, R. (2020). Emmeans: Estimated Marginal Means, Aka Least-Squares Means (R Package Version 1.4.6).
83. Fox, J., and Weisberg, S. (2019). An R Companion to Applied Regression, Third Edition (Sage Publications).
84. Brooks, M.E., Kristensen, K., Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., and Bolker, B.M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. *9*, 378–400. https://doi.org/10.32614/RJ-2017-066.
85. Bartoń, K. (2023). Mumin: Multi-model Inference (R Package Version 1.47.5).
86. Rother, M.T., Huffman, J.M., Guiterman, C.H., Robertson, K.M., and Jones, N. (2020). A history of recurrent, low-severity fire without fire exclusion in southeastern pine savannas, USA. For. Ecol. Manag. *475*, 118406. https://doi.org/10.1016/j.foreco.2020.118406.
87. Robertson, K.M., and Hmielowski, T.L. (2014). Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia *174*, 765–776. https://doi.org/10.1007/s00442-013-2823-4.
88. Brueckheimer, W.R., and Crawford, R.L. (2012). The Legacy of a Red Hills Hunting Plantation: Tall Timbers Research Station & Land Conservancy (University Press of Florida).
89. Stoddard, H. (1962). Tall Timbers Research Station Fire Ecology Plots. Tall Timbers Res. Stn. Bull. No. 2 (Tall Timbers Research Station).
90. Clewell, A.F. (2014). Forest development 44 years after fire exclusion in formerly annually burned oldfield pine woodland, Florida. Castanea *79*, 147–167. https://doi.org/10.2179/14-010.
91. Stevenson, P.R., and Vargas, I.N. (2008). Sample size and appropriate design of fruit and seed traps in tropical forests. J. Trop. Ecol. *24*, 95–105. https://doi.org/10.1017/S0266467407004646.
92. Brooke, J.M., Basinger, P.S., Birckhead, J.L., Lashley, M.A., McCord, J.M., Nanney, J.S., and Harper, C.A. (2019). Effects of fertilization and crown release on white oak (*Quercus alba*) masting and acorn quality. For. Ecol. Manag. *433*, 305–312. https://doi.org/10.1016/j.foreco.2018.11.020.
93. Hardin, J.W., and Hilbe, J. (2007). Generalized Linear Models and Extensions (Stata Press).
94. Bolker, B., Brooks, M., Gardner, B., Lennert, C., and Minami, M. (2012). Owls Example: a Zero-Inflated, Generalized Linear Mixed Model for Count Data. https://groups.nceas.ucsb.edu/non-linear-modeling/projects/owls/WRITEUP/owls.pdf/@@download.
95. Rubin, M. (2021). When to adjust alpha during multiple testing: A consideration of disjunction, conjunction, and individual testing. Synthese *199*, 10969–11000. https://doi.org/10.1007/s11229-021-03276-4.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R v4.4.0[76]	https://www.r-project.org/	N/A
R studio version 2023.9.0.463[77]	https://posit.co/download/rstudio-desktop/	N/A
R package *tidyverse*[78]	https://CRAN.R-project.org/package=tidyverse	N/A
R package *fitdistrplus*[79]	https://CRAN.r-project.org/package=fitdistrplus	N/A
R package *Dharma*[80]	https://CRAN.R-project.org/package=DHARMa	N/A
R package *performance*[81]	https://CRAN.r-project.org/package=performance	N/A
R package *emmeans*[82]	https://CRAN.R-project.org/package=emmeans	N/A
R package *car*[83]	https://CRAN.r-project.org/package=car	N/A
R package *glmmTMB*[84]	https://cran.r-project.org/package=glmmTMB	N/A
R package *Mu*min[85]	https://cran.r-project.org/package=MuMIn	N/A
Other		
Audubon Guide to North American birds	https://www.audubon.org/field-guide	N/A
The Cornell Lab: all about birds	https://www.allaboutbirds.org/guide	N/A
University of Michigan Museum of Zoology: animal diversity Web	https://animaldiversity.org/	N/A

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We conducted experiments (Table S6) at Tall Timbers Research Station (TTRS; 30°39'23.4" N, 84°12'31.5" W), a ~2800 acre property embedded alongside similarly managed properties in the Red Hills Region of the Atlantic Coastal Plain in Florida, USA. The overstory is predominantly composed of pine species (i.e., *Pinus taeda*, *Pinus echinata*, and *Pinus palustris*).[86] More forbs and off-site mesophytic woody plants occur in the understory at TTRS than in the intact longleaf pine forests that historically characterized much of the southeastern United States.[30,86,87] Most of the site has experienced annual and biennial fires applied March–May since the late 1800s and early 1900s that mimics historical fire frequency.[86,88] Fire is applied in a roughly checkerboard pattern such that units (~2–16 ha, $\bar{x} \approx 8$ ha) burned each year often abut those burned 1–2 years prior. Interspersed in this mosaic are fire-excluded experimental areas with closed canopies of primarily broadleaf trees and reduced herbaceous vegetation.

METHOD DETAILS

Experiment 1: Does frequent fire promote locally common bird-dispersed plants?

We surveyed focal plants and their fruit availability in the Stoddard Fire Plot study, a long-term experiment established in 1959 with a standardizing burn on 84 permanent ~0.20 ha plots.[36,89] This experiment consists of a randomized complete block design with three blocks and five fire frequency treatments: 1-, 2-, 3-, and 4-year return; and fire-excluded treatments.[10,36,89] We sampled three biennial spring fire plots for our frequent fire treatments and two plots left unburned since the beginning of the experiment as fire exclusion plots. We added two more fire exclusion areas using an abandoned fire phenology experiment that last burned in 1966 and another mesophytic mixed forest area not subjected to frequent fire.[90]

Plant surveys

We surveyed vegetation in the understory (height <3 m) periodically using the point-intercept method with 1 m intervals on 30 m transects on the following dates: 2020-09-02, 2021-05-22, 2022-10-25, and 2024-07-03. During individual survey events, we positioned temporary transects ~20 m apart. In total, we established 34 transects across 7 plots—3 subjected to biennial spring burns and 4 where fire is excluded (3-6 transects per site; Table S7).

Fruit production

We counted all fruit on as many as 10 randomly selected individuals belonging to focal taxa in each plot. Sampling occurred on 2022-10-04, 2022-10-25, and 2024-07-03 to account for early and late growing season fruit production. We counted fruit on 46 *C. americana*, 33 *R. copallinum*, and 20 *Rubus* spp. plants (n = 99 individuals across 7 long-term fire frequency experiment plots). The total number of individuals surveyed ranged from 5 to 24 depending on the site.

Experiment 2: Does the magnet effect increase bird activity and vectored seed rain at artificial perches?

After spring burns in 2020, we initiated a second, distinct experiment by placing three artificial perches above seed traps in each of six pairs of units (n = 36 total traps). We placed artificial perches in upland old field pine savanna, except for one unit with more hardwoods and mesic vegetation than others. We arranged the artificial perches within units and across the property to maximize site coverage while maintaining adequate distance (defined as > 500 m between sites to sample independent bird and plant assemblages and > 80 m among artificial perches within units to capture local variation). In 2021, the established paired units remained, but we swapped the burn treatment (i.e., we monitored each paired unit as <1 and 1–2 years since fire).

Artificial perches

Perches consisted of a single 15.9 mm dia. X 122 cm L. round wooden crossbar with three perpendicular 6 mm dia. X 61 cm L. wooden extensions to accommodate birds of varying sizes (Figure 1B). We positioned the perch ~2 m above the soil surface. Underneath, we constructed a 1 m^2 seed collection platform by stretching insect screening over a square PVC structure. To monitor bird activity at artificial perches, we positioned a game camera (Bushnell Trophy Cam HD) on a tripod (year 1), or wooden board affixed to a t-post (year 2) ~1.5 m from the seed traps. We oriented game cameras parallel with the artificial perch and set the trigger on high sensitivity to record 15-second videos with a 5-minute latency period between detections. We erected artificial perches, game cameras, and seed traps beginning on 2020-04-15 and sampled through 2022-04-23. We deployed game cameras and seed traps at sites sequentially as prescribed fire applications occurred in the first year of the experiment.

Avian Observations

We operated game cameras continuously during the experiment and retrieved data intermittently. In processing these video clips, we identified bird taxa, attempted to determine sex and age class (i.e., juvenile and adult), and recorded behavior. Then, we searched for taxa on Audubon Guide to North American Birds, The Cornell Lab: All About Birds, and the University of Michigan Museum of Zoology: Animal Diversity Web. Based on whether taxonomic descriptions included references to fruit or an omnivorous diet, we classified species into binary groups (i.e., potential seed dispersers and others). Some summer migrants only consume fruit in their winter range; these were considered in the 'other' category.

We calculated coverage days by subtracting the days with missing data (n = 1,931) from the total possible camera coverage days (n = 25,239). Missing data resulted from camera malfunction and misalignment, faulty traps and perches after weather events, and file formatting issues. We derived start and end dates for camera coverage from the camera deployment dates and the beginning and end of each treatment (i.e., based on the prescribed fire application dates).

Seed counts

We collected seeds from seed traps beneath artificial perches during periodic sampling events. To ensure traps remained functional during spring high-wind events in 2020, we sampled them more often in the weeks and months following fire than the rest of the year. For consistency, we continued this approach in the second year. We sampled all established pairs during field visits, resulting in 23–26 seed collections per trap, depending on when we first erected pairs (i.e., how early in the year prescribed fire occurred on that unit). After each sampling event, we attempted to identify seeds to the most refined level of taxonomic classification achievable using collected voucher specimens and tallied the number in traps. We made no attempt to ascertain seed viability. Weather, animals, and prescribed fire-damaged seed traps for brief periods of time, which prevented sample collection. We did not correct for the lack of sample collection during these periods because they were brief (<0.03% of sampling days).

Assessing assumptions and potential confounding factors in experiment 2

Avian scat observations

We recorded whether we observed birds on artificial perches defecating in game camera video clips as a binomial variable (yes/no) based on visibly observing egestion after squatting or crouching. Given the placement of the game camera directly on the artificial perch, there are no discernible environmental differences between treatments that should interfere with the observation of defecation events. We thus assumed that this data genuinely represented any differences in defecation across treatments.

Lower midstory perch availability and quality

Pine savanna vegetation is two-tiered with minimal true midstory. Fire prevents trees from growing, and many overstory species in this system naturally prune their lower branches. Consequently, the lower midstory that our trap simulates primarily consists of mostly small woody trees. Based on the height of the artificial perch (~2 m), we categorized lower midstory perches as woody plants between 1.5 and 2.5 m tall. Then, we recorded the distance from the center of each seed trap to the three nearest lower midstory perches in the dormant season of the final sampling year (2022). This procedure resulted in 18 measurements per site and 9 per paired unit (n = 108 total).

Like other distance-based, plotless methods, we assume that the distance to objects at any random point provides a measure of how often that object is likely to be encountered. We chose this over a transect method because it is more sensitive to the presence of perches immediately surrounding the seed trap, which we expected to most affect avian behavior.

The lower-midstory perches in this system have similar foliage across treatments because fire occurs early in the growing season. However, it is possible that recent fire results in mortality, which would create differences in foliage and therefore perch quality. We thus recorded the presence or absence of foliage on our perches after the growing season (n = 105 individuals). We note that evergreen perches may have had foliage in the 1–2 years since fire units before similar individuals in the <1 year since fire began growing new leaves. Such species account for ~13% of the data.

Calculating fruit availability

We quantified fruit availability by recording the presence of fruit as a binomial variable on three 1 m point vegetation transects at traps for each of *Rubus* spp., *C. americana*, and *R. copallinum*. We sampled traps in each site in <1 year since fire and 1–2 years since fire once at a minimum (n = 519 transects). This resulted in 72 surveys at traps for *Rubus* spp., 60 for *C. americana*, and 42 for *R. copallinum*. The size of these transects depended upon the relative abundance of focal plants (5 m for *Rubus* spp.; 30 m for *C. americana* and *R. copallinum*).

Seed loss probability

We developed a general metric (i.e., not species-specific) to estimate an expected seed rain that accounted for differences in the effect of seed loss across treatments, similar to approaches used in other.[91,92] Seed morphology may also influence seed loss, so we selected three species that varied in physiological and morphological traits to use in seed loss trials. During the first growing season (2020-04-06–2020-07-26), we placed a known quantity of seeds into seed traps during six sequential trials that varied in length (6–23 days). For each trial, we spread 10 bell pepper (*Capsicum annuum*, Ferry-Morse®), yellow mustard (*Sinapis alba*, Outsidepride®), and sunflower (*Helianthus annuus*, Royal Wing®) seeds onto the collection surface (n = 30 total). Upon returning for the next collection, we tallied the remaining seeds.

QUANTIFICATION AND STATISTICAL ANALYSIS

Modeling approach

We cleaned, analyzed, and visualized data using R version 4.4.0.76 and R studio version 2023.9.0.463.[77] We conducted models using the glmmTMB function from the glmmTMB package.[84] First, we evaluated the distribution of response variables to determine mean-variance relationships. For negative binomial distributions, we also visually inspected the relationship between mean and variance to select the appropriate parameterization.[93,94] Then, we chose the convergent model that best incorporated our nested experimental design while satisfying model assumptions. For the second experiment, we prioritized accounting for non-independence at the landscape scale (e.g., site), followed by individual traps (e.g., ID) and then units composing the pairs (i.e., sites). After selecting a model, we extracted estimated marginal means, confidence intervals, and measures of effect size. We adjusted these marginal means using a sigma value calculated as the square root of the sum of squared variance values for random effects. This procedure was omitted for models with an overdispersion term because high variance produced unreliable estimated marginal means. For ANOVAs on model objects, type depended on whether the hypothesis focused on main effects (type II) or an interaction (type III). We did not correct for multiple comparisons for any analysis involving multiple species. Corrections are appropriate for disjunction testing, in which one statistically significant result is sufficient to reject the joint null hypothesis.[95] Instead, we assessed the hypothesis independently for each species. Finally, we derive explained variance using the r.squaredGLMM function from the MuMIn package.[85] We report the range of values produced using the delta (typically more conservative), trigamma, and lognormal methods for count data, and the delta and theoretical methods for binomial data.

Experiment 1: Does frequent fire promote locally common bird-dispersed plants?

Plant surveys

We modeled the number of transect points with focal taxa (i.e., *C. americana*, *R. copallinum*, and *Rubus* spp.) using a negative binomial general linear mixed effects model (GLMM) with variance = $\mu\left(1+\frac{\mu}{\kappa}\right)$, where μ is the mean and κ an overdispersion parameter (type 2 hereafter). The number of total transect points are censored, which violates the Poisson distribution assumption of unbounded counts. However, the Poisson model is appropriate in this case because the number of transect points with focal taxa never approached the maximum possible points. The model included the factors treatment (biennial fire, fire exclusion) and focal taxa as fixed effects and the random effect of plot as a factor nested within treatment. We conducted a global model to estimate marginal means but *R. copallinum* and *Rubus* spp. did not occur in both treatments. We thus also conducted a reduced model to compare *C. americana* across treatments and assessed it using type II ANOVA:

$$\#\text{Transect points (all focal taxa)} \sim \text{Treatment} * \text{Focal taxa} + \left(1|\,\text{Treatment}/_{\text{Plot}}\right)$$

$$\#\text{Transect points } (C.\ americana) \sim \text{Treatment} + \left(1|\,\text{Treatment}/_{\text{Plot}}\right)$$

Understory plants in our system are more abundant overall with recurring fire than with fire exclusion. To evaluate the relative contribution of focal taxa to the composition of plant communities, we created a binomial variable describing whether plants detected at individual points along transects belonged to our focal did (success, failure). Then, we summarized the total number of successes and failures for focal taxa in each plot and conducted a binomial GLMM. The model included the factors treatment (biennial fire, fire exclusion) and focal taxa as fixed effects and the random effect of plot (1-7) as a factor nested within treatment. We conducted a global model to estimate marginal means, but *R. copallinum* and *Rubus* spp. were absent with fire exclusion. We thus also conducted a reduced model to compare *C. americana* across treatments and assessed it using type II ANOVA:

$$\text{Successes, \# Failures(all taxa)} \sim \text{Treatment} * \text{Focal taxa} + \left(1|\,\text{Treatment}/_{\text{Plot}}\right)$$

$$\#\text{Successes}, \#\text{Failures}(\textit{C. americana}) \sim \text{Treatment} + \left(1 | \text{Treatment}_{/\text{Plot}}\right)$$

Fruit production

We determined how long-term biennial fire and fire exclusion influenced fruit production for individual focal plants with a type 2 negative binomial GLMM. We conducted a global model including the factors treatment (biennial fire, fire exclusion) and focal taxa (*C. americana*, *R. Copallinum*, and *Rubus* spp.) as fixed effects and the random effect of plot (1-7) as a factor nested within treatment. We detected *R. copallinum* and *Rubus* spp. individuals in fire exclusion, but none produced fruit. We thus also conducted a reduced model to compare *C. americana* fruit production across treatments and assessed it using a type II ANOVA. We had to drop plot as a predictor for this model to converge:

$$\#\text{of fruit per individual (all taxa)} \sim \text{Treatment} * \text{Focal taxa} + (1|\text{Treatment}/\text{Plot})$$

$$\#\text{of fruit per individual } (\textit{C. americana}) \sim \text{Treatment}$$

Experiment 2: Does the magnet effect increase bird activity and vectored seed rain at artificial perches?

Model design

The models below parallel the experimental design. They include the factors treatment (<1 or 1–2 years since fire) and year of fire application (first or second) as fixed effects and the factors site (1-6), unit (A-L) and individual trap ID (1-36) as nested random effects. The random effects in the model account for the 36 individual traps (ID) nested within 12 units that are themselves nested within 6 sites (Figure 1A). This model specification accounts for local variation in avian activity and seed rain at artificial perches with a paired analysis isolating the effects of fire at individual traps (two measurements at each trap, one in each treatment year). Including trap ID as a random effect results in a model that attributes less variance to fixed effects. This is a conservative approach that addresses non-independence.

Avian observations

We retained observations for species consuming fruit to any degree in our system and analyzed all potential fruit-consuming birds together. After summarizing total observations at traps for each treatment year (i.e., <1 and 1–2 years since fire in each of the two sampling years), we conducted a type 2 negative binomial GLMM. To account for coverage differences resulting from camera malfunction and misalignment, periods of perch unavailability due to weather or fire, and file formatting issues, we also incorporated a log-transformed offset term for camera coverage days (158–383) in each treatment year. We assessed this model using type II ANOVA:

$$\text{Avian observations} \sim \text{Treatment} * \text{Burn year} + (1|\text{Site}) + (1|\text{Site}/\text{Unit}) + (1|\text{Site}/\text{Unit}/\text{ID}) + \text{offset}(\log(\text{Coverage days}))$$

Expected seed counts

We calculated raw annual seed totals by summarizing counts of focal taxa (C. *americana*, *R. copallinum*, and *Rubus* spp.) over treatment years at individual traps. We modeled GLMMs with a type II negative binomial distribution and repeated this analysis using counts adjusted for differences in seed loss, fruit availability, and their combined effect (see below). A model including the full nested experimental design (i.e., unit) was singular. We assessed the model using type III ANOVA:

$$\text{Seed counts} \sim \text{Treatment} * \text{Species} * \text{Burn year} + (1|\text{Site}) + (1|\text{Site}/\text{ID})$$

Examining assumptions and potential confounding factors in experiment 2

Avian defecation observations

We modeled the probability of observing any defecation events by potential seed-dispersing birds in individual videos recorded at artificial perches. With this binomial response variable, we conducted a binomial GLMM with fire treatment and burn year as interacting fixed effects and site (1-6) and trap ID as nested random effects. A model including the full nested experimental design (i.e., unit) was singular. We assessed the model using type II ANOVA:

$$\#\text{Defecation observations}, \#\text{Failures} \sim \text{Treatment} * \text{Burn year} + (1|\text{Site}) + (1|\text{Site}/\text{ID})$$

Lower midstory perch availability and quality

We conducted a GLMM to estimate distance to the nearest perch using the gaussian distribution with a log link. The model included the fixed factor fire treatment and the random factors site and trap ID. We assessed the model using type II ANOVA:

$$\text{Distance} \sim \text{Treatment} + (1|\text{Site}/\text{ID})$$

We also conducted a binomial GLMM to estimate the probability of observing foliage on the lower midstory perches. The model included the binomial response variable of foliage (yes/ no), the fixed effect factor of treatment (<1 year since burn, 1–2 years since burn), and the random effect factor of site (1-6). A model including the full nested experimental design was singular. We assessed the model using type II ANOVA:

$$\text{Foliage}(\text{y}/\text{n}) \sim \text{Treatment} + (1|\text{Site})$$

Calculating fruit probability

We conducted binomial GLMMs to estimate the probability of detecting fruit at each point of 1 m point-intercept vegetation transects. This model included a binomial response based on whether focal plants at transect points bore fruit during surveys in each treatment year. Fixed effects included the factors burn treatment (<1 year since burn, 1–2 years since burn) and species (*C. americana*, *R. copallinum*, *Rubus* spp.). Random effects included the factor site (1-6), unit (A-L) and an overdispersion term. We assessed this model using type III ANOVA for interactions between treatment and species:

$$\#\text{Transect Points with Fruit}, \#\text{Total Transect Points} \sim \text{Treatment} * \text{Species} + (1|\text{Site}/\text{Unit}) + (1|\text{Overdispersion term})$$

Based on this model, we calculated the ratio of fruit availability for <1 year since fire compared to 1–2 years since fire using estimated marginal means for each focal taxa (Lenth, 2020).[82] The marginal means are point estimates within a range of variation. A limitation of this approach is that it then propagates uncertainty that is not quantified in the resulting ratio. We multiplied raw seed rain by this ratio:

$$Ratio = \frac{Fruit\ observation\ probability_{1-2\ years\ since\ fire}}{Fruit\ observation\ probability_{<1\ year\ since\ fire}}$$

Seed loss probability

We conducted binomial GLMMs to estimate the probability of seed loss from seed traps beneath artificial perches. This model included a binomial response variable for seed loss; the fixed effects treatment (<1 year since burn, 1–2 years since burn), trial (1-6), and species (*C. annuum*, *S. alba*, and *H. annuus*); the fixed continuous predictor trial length (6–28 days), and the random effects site (1-6) and trap ID (1-36). We included an interactive term between trial and treatment to account for any variation in the effect of fire across time because the trials were sequential. The model required an overdispersion term and was singular when including the completed nested structure of the experimental design (e.g., unit). We assessed this model using type II ANOVA:

$$\#\text{Lost Seeds}, \#\text{Starting Seeds} \sim \text{Treatment} * \text{Trial} + \text{Trial length} + \text{Species} + (1|\text{Site}) + (1|\text{Site}/\text{Trap}) + (1|\text{Overdispersion term})$$

Based on this model, we again calculated the ratio of seed loss for <1 year since fire compared to 1–2 years since fire using estimated marginal means (Lenth, 2020).[82] We multiplied raw seed rain by this ratio and by projected totals after adjusting for fruit availability:

$$Ratio = \frac{1 - seed\ loss\ probability_{1-2\ years\ since\ fire}}{1 - seed\ loss\ probability_{<1\ year\ since\ fire}}$$