

Effects of management outweigh effects of plant diversity on restored animal communities in tallgrass prairies

Peter W. Guiden^{a,1}, Nicholas A. Barber^b, Ryan Blackburn^c, Anna Farrell^a, Jessica Fliginger^a, Sheryl C. Hosler^d, Richard B. King^{a,e}, Melissa Nelson^a, Erin G. Rowland^a, Kirstie Savage^a, John P. Vanek^a, and Holly P. Jones^{a,e}

^aDepartment of Biological Sciences, Northern Illinois University, DeKalb, IL 60115; ^bDepartment of Biology, San Diego State University, San Diego, CA 92182; ^cSchool of Forestry, Northern Arizona University, Flagstaff, AZ 86011; ^dDepartment of Biological Sciences, University of Illinois at Chicago, Chicago, IL 60607; and ^eInstitute for the Study of the Environment, Sustainability and Energy, Northern Illinois University, DeKalb, IL 60115

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A primary goal of ecological restoration is to increase biodiversity in degraded ecosystems. However, the success of restoration ecology is often assessed by measuring the response of a single functional group or trophic level to restoration, without considering how restoration affects multitrophic interactions that shape biodiversity. An ecosystem-wide approach to restoration is therefore necessary to understand whether animal responses to restoration, such as changes in biodiversity, are facilitated by changes in plant communities (plant-driven effects) or disturbance and succession resulting from restoration activities (management-driven effects). Furthermore, most restoration ecology studies focus on how restoration alters taxonomic diversity, while less attention is paid to the response of functional and phylogenetic diversity in restored ecosystems. Here, we compared the strength of plant-driven and management-driven effects of restoration on four animal communities (ground beetles, dung beetles, snakes, and small mammals) in a chronosequence of restored tallgrass prairie, where sites varied in management history (prescribed fire and bison reintroduction). Our analyses indicate that management-driven effects on animal communities were six-times stronger than effects mediated through changes in plant biodiversity. Additionally, we demonstrate that restoration can simultaneously have positive and negative effects on biodiversity through different pathways, which may help reconcile variation in restoration outcomes. Furthermore, animal taxonomic and phylogenetic diversity responded differently to restoration, suggesting that restoration plans might benefit from considering multiple dimensions of animal biodiversity. We conclude that metrics of plant diversity alone may not be adequate to assess the success of restoration in reassembling functional ecosystems.

biodiversity | bison | prescribed fire | restoration ecology | structural equation model

Earth's biodiversity is rapidly disappearing (1, 2), and as a consequence, ecosystem function is eroding across the planet (3, 4). Ecological restoration has emerged as an important strategy to slow or reverse biodiversity losses (5–8) with its global importance underscored by the United Nations proclaiming 2021 to 2030 the “Decade on Ecosystem Restoration.” One common metric used to assess the success of this substantial global investment is the recovery of biodiversity (9, 10). While many studies report positive effects of restoration on biodiversity, these studies typically focus either on the response of plant or animal communities, but rarely both (5, 11–13). This focus on component pieces of ecosystems makes it difficult to identify ecosystem-wide responses of biodiversity to restoration at multiple trophic levels (14–16).

In the absence of multitrophic restoration studies, the Field of Dreams hypothesis (“if you build habitat, animals will come”) (17) has become a rarely tested paradigm of restoration ecology

(18–20). A key prediction of the Field of Dreams hypothesis is that restoring plant biodiversity leads to passive recovery of animal biodiversity (21–23). Consequently, restoring historical disturbance regimes and soil conditions that maximize plant biodiversity is the central goal of many restoration plans (e.g., periodic inundation in wetland restorations) (24, 25). Evidence for correlations between plant and animal biodiversity is equivocal, however. Plant biodiversity is often a poor predictor of animal biodiversity once productivity or abiotic factors, such as nutrient concentrations and precipitation, are controlled for (26–29). Additionally, variables describing the quantity or quality of animal habitat, including landscape configuration (30–32) or structural heterogeneity (26, 33, 34), commonly exhibit stronger correlations with animal biodiversity. Management practices focused on restoring plant communities may therefore be insufficient to also restore animal communities (35, 36) and risk falling short of the ultimate goal of entire-ecosystem restoration (13, 37–40). Critical tests of the Field of Dreams hypothesis are therefore needed to improve both restoration science and our

Significance

“If you build it, they will come” is a commonly accepted principle of restoration ecology (the Field of Dreams hypothesis). This hypothesis, which frequently guides restoration practice, predicts that restoring plant biodiversity will lead to the recovery of animal biodiversity. However, this prediction is rarely tested because restoration studies measure plant or animal biodiversity, but rarely both. Four years of plant and animal biodiversity data collected from tallgrass prairies showed that restoration had strong effects on vertebrate and invertebrate biodiversity. Animal biodiversity was explained more by management practices than plant biodiversity, demonstrating important responses not captured by the Field of Dreams hypothesis. Where animals mediate key ecosystem functions, restoration planning will benefit from explicitly considering the responses of animal communities.

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¹To whom correspondence may be addressed. Email: pguiden@niu.edu.

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understanding of how multitrophic interactions and disturbance jointly structure biodiversity (3, 13, 36, 41).

Here, we classify the effects of restoration on animal biodiversity into two broad mechanisms, which we refer to as plant-driven effects and management-driven effects (Fig. 1). Plant-driven restoration effects (Fig. 1A and B) primarily represent animals partitioning diverse food resources provided by vegetation or habitat diversity (27, 36, 42). On the other hand, management-driven restoration effects (Fig. 1C) represent animals responding to changes in habitat quantity (43), quality (44), and structure (45–47) resulting from successional changes, legacy effects, and disturbance regimes used in restoration. While the exact classification of restoration effects will vary with the temporal, spatial, and taxonomic scale of a restoration project or ecological study, partitioning these effects into multiple pathways allows for a more precise description of community responses to restoration (16, 48).

Comparing plant-driven and management-driven effects of restoration could also identify important processes that are obscured in studies focused on a single species or trophic level. For example, a lack of correlation between animal biodiversity and restoration disturbance regimes might be interpreted as evidence that restoration has no effect on biodiversity (10). However, this pattern could also arise when disturbance has strong positive management-driven effects and strong negative plant-driven effects, or vice versa (27). Spatial and temporal variation in environmental conditions that affect the strength of either management-driven or plant-driven effects (49, 50) may therefore lead to unanticipated shifts in animal communities. Additionally, a strong correlation between management and animal biodiversity could be the product of either management-driven

or plant-driven effects, both of these pathways, or complex interactions among the two (36, 41, 51). Disentangling management-driven and plant-driven restoration effects will therefore require carefully designed experiments or statistical analyses (52). Doing so could help reconcile discrepancies in and better predict restoration outcomes (53).

Our objective was to understand how ecological restoration can affect biodiversity in a wide range of animal communities (ground beetles, dung beetles, snakes, and small mammals). These animal communities comprise a substantial amount of biodiversity in tallgrass prairies and support important ecosystem functions such as nutrient transfer (dung beetles) (54), top-down control of weedy plants (ground beetles) (55) and herbivores (snakes) (56), and support of predator populations (small mammals) (57). As one of the most globally imperiled ecosystems (58), tallgrass prairies are actively restored using both revegetation (e.g., direct seeding of native plants) (25) and reinstating historical abiotic- and biotic-disturbance regimes (e.g., prescribed fire and reintroducing *Bison bison*, a keystone herbivore) (59). We simultaneously monitored plant and animal biodiversity in sites that varied in age (i.e., time since restoration) and restoration disturbance regimes (i.e., time since prescribed fire and bison presence). We then used these data to parameterize structural equation models to test a central prediction of the Field of Dreams hypothesis—that increasing plant biodiversity leads to increased animal biodiversity (24). Specifically, we tested whether the effects of restoration on animal taxonomic diversity (based on the relative abundance of species) and phylogenetic diversity (weighted by phylogenetic distance among species) were mediated by changes in plant taxonomic, phylogenetic, and functional diversity following restoration. Consistent with the Field of Dreams hypothesis, we predicted that the strength of plant-driven restoration effects on animal biodiversity would be stronger on average than any management-driven restoration effects.

Methods

Study Area. This research was conducted at Nachusa Grasslands in Franklin Grove, IL (41.891°N, 89.343°W), a 1,500-hectare nature preserve consisting of restored and remnant prairies, oak savanna, and wetlands managed by The Nature Conservancy. We collected data from 17 60 × 60 m long-term research sites in restored prairies that were established in 2013 as part of the Restoring Function in Grassland Ecosystems project (44, 45). Restoration began in 1987, when direct seeding was used to transition sites from row-crop agriculture to tallgrass prairie (60). These sites fall along a chronosequence of restoration age, spanning 3 to 32 y since restoration. Each site experienced a unique burn history, as a subset of sites are burned each year in either spring or fall. For each year of our study, we estimated the time since burn (in months) for each site from June of that year. The mean time since burn was 10.4 ± 11.0 mo (mean $\pm$ SD) because most sites were burned either the preceding spring or spring of the previous year. Sites also vary in their grazing history. Bison were reintroduced to eight sites between 2014 and 2015 in order to reinstate historical disturbance regimes that maintained prairies prior to European conquest (59). For more details of the study area, see ref. 60.

Field Surveys. Plant communities were surveyed annually in August from 2016 to 2019 (SI Appendix, Table S1). At 10 randomly selected points in each site, we estimated percent cover of all plant species in a 0.5×0.5 m quadrat each year. In order to quantify plant functional diversity, we measured several traits that are linked to ecosystem function (e.g., primary productivity) in the 10 most abundant plant species in each grid (by absolute plant cover). Specifically, we measured growth form (e.g., forb, legume, C₃ grass, or C₄ grass), height, specific leaf area and leaf toughness, area, dry matter content, percent C, and percent N (61).

Ground beetle and dung beetle communities were surveyed from 2017 to 2018 using pitfall traps (54, 62). Two pitfall trap arrays, which consisted of five pitfall traps spaced 5 m apart, were deployed at each site. Dung beetle pitfall traps were baited with bison dung on a fork balanced over top of the trap. Traps were deployed three times a year (May/June, July, and September) for 1 to 3 wk. For analysis, we calculated the total number of captured beetles per species divided by effort (the number of trap-days at each site during each year).

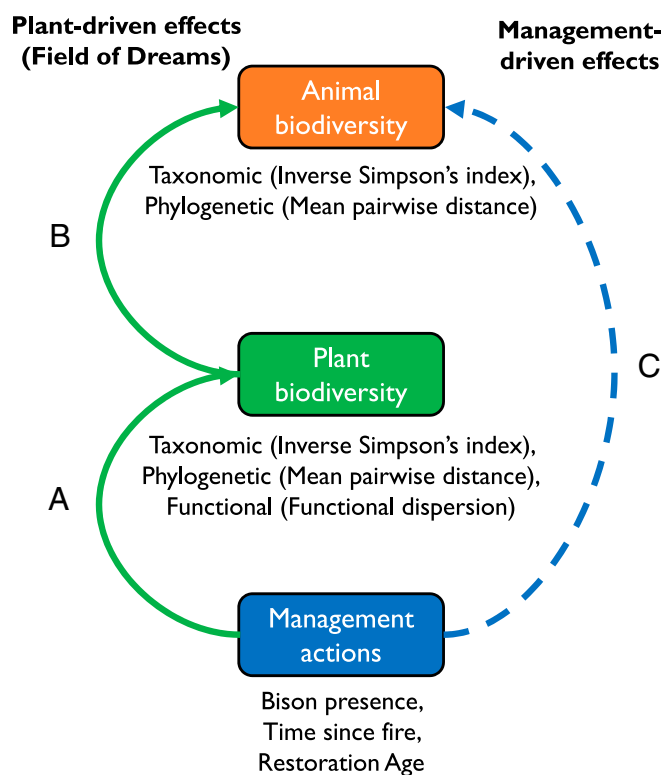


Fig. 1. Conceptual metamodel illustrating a key prediction of the Field of Dreams hypothesis: restoration changes plant diversity (A), which in turn shapes animal biodiversity (B). Alternatively, restoration practices might also have strong management-driven effects on animal biodiversity that are independent of changes in plant biodiversity (C). The text indicates specific restoration approaches and dimensions of biodiversity tested in this study.

Snake communities were surveyed at 12 sites in 2016. Each site had two transects of 10 artificial cover objects (ACOs) (56). Transects were placed in the center of each site (not necessarily coincident with long-term monitoring sites) with >50 m between transects and 20 m between ACOs. ACOs were checked approximately weekly between May and October, and captured snakes were marked by clipping ventral scales. We summed the total number of unique individuals per 100 ACO checks for each species.

Small mammal communities were surveyed from 2016 to 2019 using mark-recapture techniques. We deployed 5 × 5 grids of Sherman live-traps at each site for four consecutive nights four times per year (April, June, August, and October; *SI Appendix, Table S1*) (45). At each site, we then summed the total number of captured individuals (M_{t+1}) (63) of each species each year, correcting for unequal trap effort.

Biodiversity Metrics. We used abundance data to quantify variation in multiple dimensions of plant and animal biodiversity. Taxonomic, phylogenetic, and functional diversity metrics were calculated separately for each community, as each represents an evolutionarily and ecologically distinct group (plants, small mammals, snakes, dung beetles, and ground beetles). All data were analyzed in R version 3.6.1 (64). We measured the inverse Simpson's index for all taxa at each site using the "vegan" package (65), hereafter referred to as taxonomic diversity. We obtained a phylogeny for dung beetles (66), snakes (67), and mammals (68); there was no available phylogeny for ground beetles at our site (*SI Appendix, Table S1*). We used these phylogenies to calculate abundance-weighted phylogenetic distance matrices from which we calculated standardized-effect size mean pairwise distance at each site using the "picante" package (69), hereafter referred to as phylogenetic diversity. Mean pairwise distance quantifies phylogenetic divergence (i.e., communities where common species are distant evolutionary relatives have higher values) (70). We also measured functional dispersion in all plant communities, which reflects the average distance in multivariate trait-space between all species and the community centroid. As species in a community become more functionally dissimilar, functional dispersion increases (71). We calculated functional dispersion using the mean value of functional traits for each species in the "FD" package (72), hereafter referred to as functional diversity. Because animal functional diversity was highly correlated with animal taxonomic diversity in our data (*SI Appendix, Fig. S4*), we did not include it in our final analyses.

Statistical Analysis. We tested the effects of management on animal community biodiversity using piecewise structural equation models (piecewiseSEM) (73). In structural equation modeling, theory is used to construct a network of relationships among variables. These hypothesized causal paths are then evaluated against the data by combining inferences across multiple regression models and overall model fit evaluated by testing the significance of missing (i.e., unspecified) causal paths (high P values represent a well-supported model). By allowing response variables to be used as predictor variables in subsequent models, structural equation models can be used to compare the strength of compound effects with multiple paths (e.g., plant-driven effects, Fig. 1 A and B) to simple effects with a single path (e.g., management-driven effects, Fig. 1C) (74, 75). Structural equation models describing the effect of restoration on animal biodiversity were constructed separately for each animal community ($n = 4$ sets of structural equation models). Our first structural equation model for each taxon reflected the null hypothesis that only plant-driven effects influence animal biodiversity (i.e., the Field of Dreams hypothesis, Fig. 1). According to this null hypothesis, animal taxonomic diversity and animal phylogenetic diversity (for all taxa except ground beetles) were treated as endogenous variables (i.e., variables explained by other variables in the model) that depended only on plant taxonomic diversity, plant phylogenetic diversity, and plant functional diversity. Plant biodiversity was also treated as an endogenous variable that responded to restoration: we included a path for each dimension of plant biodiversity (taxonomic, phylogenetic, and functional) to each management action (restoration age, time since burn, and bison). We treated bison as a categorical variable in our analysis (bison present or bison absent). Continuous measures of bison activity (dung counts) conducted on a subset of our data provided similar results (*SI Appendix, Tables S3–S6*). For all taxa except ground beetles (for which we only calculated taxonomic diversity), we included a correlated error term for animal taxonomic and phylogenetic diversity.

Each structural equation model was fit to field data using either general linear models in taxa with only 1 y of data (snakes) or linear mixed-effects models that included a random intercept for site in taxa with multiple years of data (ground beetles, dung beetles, and small mammals). We then tested for missing paths (i.e., strong management-driven effects on animal

biodiversity) using d-separation tests. D-separation tests check the assumption that unconnected variables are conditionally independent (73). We added missing paths in which $P < 0.05$. For all final structural equation models, we assessed model fit using Fisher's C , which integrates all d-separation tests (73). While Fig. 2 summarizes our general findings, the strength of each individual path can be found in *SI Appendix, Fig. S5 and Tables S7–S11*. Relationships between variables are reported as range-standardized path coefficients, which are analogous to regression coefficients (74). Unstandardized path coefficients are provided in *SI Appendix, Tables S7–S11*. We tested path coefficients for statistical significance using P values. For mixed models, path coefficient P values were derived using the Kenward-Rogers approximation for denominator degrees of freedom (76). We report R^2 , which was calculated using the piecewiseSEM package (73), for each component model of all structural equation models in *SI Appendix, Fig. S5*.

We used the final structural equation models for each animal taxon to compare the strength of plant-driven and management-driven effects of restoration on animal biodiversity. We extracted all path coefficients from the final set of models. Plant-driven effects (Fig. 1 A and B) were calculated as compound paths between management and animal biodiversity (e.g., the product of the path linking management and plant biodiversity and the path linking plant biodiversity and animal biodiversity) (75). Management-driven effects were calculated as any single-path coefficient linking management action to animal biodiversity (Fig. 1C). We modeled the magnitude of standardized path coefficients (log-transformed to meet model assumptions) as a function of path type (plant-mediated effect or direct effect) and present these results as means $\pm$ SE.

Results

We found strong support for our structural equation models describing the biodiversity of ground beetles (Fisher's $C = 0.73$, $P = 0.69$, and degrees of freedom [d.f.] = 2), dung beetles (Fisher's $C = 3.67$, $P = 0.72$, and d.f. = 6), snakes (Fisher's $C = 6.96$, $P = 0.72$, and d.f. = 10), and small mammals (Fisher's $C = 6.88$, $P = 0.73$, and d.f. = 10) in response to variation in restoration (Fig. 2 and *SI Appendix, Fig. S5*). Each animal community differed considerably in its specific responses to restoration. Ground beetle taxonomic diversity decreased in older restorations (range-standardized path coefficient: -0.524 , $P = 0.03$) and in response to bison (-0.184 , $P = 0.05$) but increased with plant taxonomic diversity (0.541 , $P = 0.007$). Dung beetle taxonomic diversity increased with restoration age (0.757 , $P < 0.001$) but decreased with time since burn (-0.410 , $P < 0.001$) and plant phylogenetic diversity (-0.331 , $P = 0.01$). Dung beetle phylogenetic diversity decreased in the presence of bison (-0.176 , $P = 0.05$) and plant phylogenetic diversity (-0.331 , $P = 0.06$). Snake taxonomic diversity increased with plant taxonomic diversity (1.321 , $P = 0.002$) and plant functional diversity (0.870 , $P = 0.01$) but marginally decreased with plant phylogenetic diversity (-0.502 , $P = 0.09$). Snake phylogenetic diversity decreased with restoration age (-1.075 , $P = 0.06$) and marginally increased with plant functional diversity (0.867 , $P = 0.09$). Small mammal taxonomic diversity increased with time since fire (0.483 , $P < 0.001$) but also weakly increased with plant functional diversity (0.350 , $P = 0.07$). Small mammal phylogenetic diversity increased with plant functional diversity (0.520 , $P = 0.05$) but decreased with plant phylogenetic diversity (-0.446 , $P = 0.03$). On average, the magnitude of management-driven effects on animal biodiversity (mean $\pm$ SE: 0.430 ± 0.167) was six-times stronger than plant-mediated effects (0.078 ± 0.017 , $F_{1,26} = 14.26$, $P < 0.001$, Fig. 3).

Discussion

The ecological mechanisms driving responses to restoration are often unclear, particularly for animal communities (11, 38). Restoration studies rarely explore how trophic interactions might shape community responses to restoration (13, 38, 77), but it is often assumed that restoring plant biodiversity is sufficient to restore functioning ecosystems. While this prediction of the Field of Dreams hypothesis was generally supported by our data, management-driven effects, capturing animal responses to

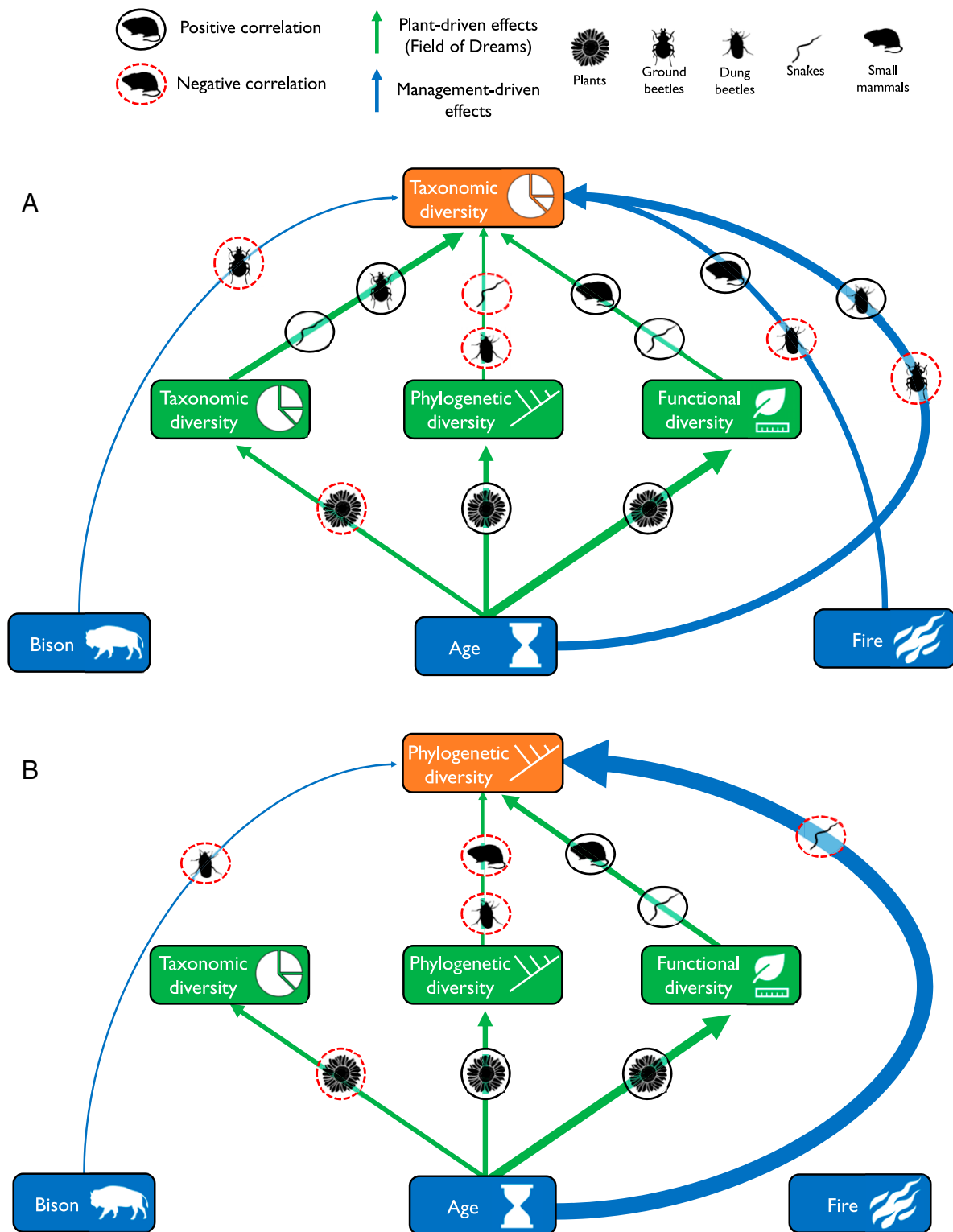


Fig. 2. Visualization of the most important paths linking restoration approaches (blue), plant biodiversity (green), and animal biodiversity (orange) in restored tallgrass prairie ecosystems. The path diagrams depict how restoration affected (A) taxonomic diversity and (B) phylogenetic diversity of ground beetles, dung beetles, snakes, and small mammals. For simplicity, only paths where $P < 0.10$ are shown here (see *SI Appendix, Fig. S5* for all paths). The width of the paths is proportional to the mean absolute value of range-standardized path coefficients; thicker arrows indicate stronger effects. Icons show which animals were affected by each path. Icons outlined by black lines had positive path coefficients, and icons outlined by red lines had negative path coefficients. Blue lines indicate management-driven effects of restoration, while green lines indicate plant-driven effects. Note that *A* and *B* reflect the output of a single structural equation model for each taxa (small mammals: $n = 67$; snakes: $n = 12$; dung beetles: $n = 34$; ground beetles: $n = 34$).

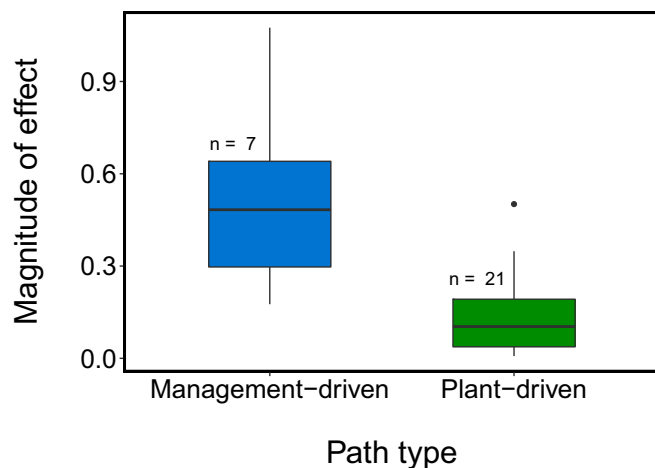


Fig. 3. The magnitude of management-driven effects of restoration on animal biodiversity (blue, $n = 7$) was more than six-times greater than plant-driven effects (green, $n = 21$; $F_{1,26} = 14.26$, $P < 0.001$). Effect sizes were calculated using the absolute value of structural equation model standardized path coefficients.

disturbance and succession, were consistently more important than effects mediated through changes in plant biodiversity (Fig. 3). Additionally, we demonstrate that restoration can have opposing management-driven and plant-driven effects on animal biodiversity (Fig. 2). Finally, taxonomic and phylogenetic biodiversity rarely responded similarly to restoration (Fig. 2), highlighting the importance of considering multiple dimensions of biodiversity. We conclude that metrics of plant biodiversity alone may not be adequate to assess the success of restoration in reassembling functional ecosystems.

Local Variation in Animal Biodiversity Is Shaped by Disturbance rather than Plant Biodiversity. Disturbance and succession can shape animal biodiversity (78–80) by changing 1) habitat quantity, quality, or structure (33, 81) and 2) plant biodiversity, which alters the diversity, quantity, or distribution of resources (36, 42). By simultaneously measuring plant and animal responses to restoration disturbances, our study was able to disentangle these two pathways, providing a rare comparison of management-driven and plant-driven effects on animal biodiversity. In both vertebrate and invertebrate communities, animal biodiversity was predominantly shaped by management-driven effects, including disturbances associated with restoration (prescribed fire and bison grazing) and restoration age. Although plant biodiversity influenced animal biodiversity in some cases (Fig. 2 and *SI Appendix, Fig. S5*), plant-driven effects were generally much weaker than management-driven effects (Fig. 3).

We likely observed relatively weak plant-driven effects of restoration because many of the animals studied are decomposers (dung beetles), omnivores (small mammals), or carnivores (snakes and ground beetles). Animal communities composed of herbivores, particularly species with a high degree of host specificity, may show stronger relationships to plant diversity (42, 82). Additionally, measuring multiple dimensions of fire and bison activity might highlight further effects on animal diversity. For example, variation in soil temperatures or loss of soil carbon following fire may determine how prescribed burns affect belowground habitat quality for insects (83, 84), and bison wallowing and grazing may have distinct effects on the availability and structure of aboveground habitat (85). Restoration projects will therefore benefit from considering the wide-ranging effects of these disturbances on animal biodiversity.

These strong direct effects of restoration disturbance on animal biodiversity highlight two important shortcomings of the Field of Dreams hypothesis that have implications for ecological restoration. First, even if a habitat is built, animals may not come because of dispersal limitation. Restoration plans commonly use direct seeding or seedling planting to alleviate dispersal limitation in plants (86), but animal propagules are rarely purposefully introduced in restoration (30). This explains the strong effect of restoration age on ground beetle and dung beetle taxonomic diversity and snake phylogenetic diversity (Fig. 2). In these taxa, older sites were more likely to be colonized by dispersal-limited species (56, 62). This suggests that considering landscape connectivity and habitat patch isolation may help predict animal community responses to restoration (87, 88). Second, effective restoration requires understanding animal habitat requirements. For example, annual burning prevents grass-litter accumulation, which is a critical habitat feature for grassland specialists such as *Microtus ochrogaster* (prairie vole) (45). The most diverse small-mammal communities were therefore found in sites that had not recently been burned (*SI Appendix, Fig. S5*). Where the recovery of ecosystem functions supported by animal biodiversity is an explicit restoration goal (89, 90), it will be important to increase focus on the direct effects of restoration on animal communities. However, balancing multiple perspectives may occasionally lead to conflicts between plans to maximize plant and animal biodiversity, such as high rates of seed predation by granivores (13, 40, 91). This reinforces the importance of establishing well-defined goals prior to initiating restoration projects and considering the context dependency of restoration goals (24, 92, 93).

While we focused on the response of biodiversity to restoration, other aspects of animal communities may have important responses that should be considered when assessing the success of restoration projects (11, 94). A goal of increasing the occupancy, abundance, or fitness of rare or functionally important species might have higher priority than increasing animal biodiversity in some cases, as the functional identity of dominant species can control ecosystem processes (37, 39, 95). For example, bison decreased dung beetle phylogenetic diversity because of an increase in large-bodied *Onthophagus* species (Fig. 2*B*), which are likely responsible for more dung decomposition than smaller species (54, 96, 97). Understanding the extent to which ecosystem functions are mediated by the community as a whole versus individual species or genotypes will therefore be important for effectively restoring animal communities that support ecosystem functions and services (98, 99).

Disturbance Can Shape Animal Biodiversity through Multiple Opposing Pathways. Our analysis detected several instances where restoration had opposing management-driven and plant-driven effects on animal biodiversity. For example, we observed a negative management-driven effect of restoration age on snake phylogenetic diversity. However, this was countered by a positive plant-driven effect of restoration age on snake phylogenetic diversity mediated by plant functional diversity (Fig. 2*B* and *SI Appendix, Fig. S5*). Decreases in snake phylogenetic diversity were driven by increased *Storeria dekayi* (DeKay's brownsnake) abundance in older sites, a dispersal-limited species that takes longer to reach restored habitat than larger snake species (56). However, functionally diverse plant communities (often older sites) likely contain a more diverse prey base that supports snake species with different foraging preferences (56). Similarly, we observed both a positive management-driven effect and negative plant-driven effect of restoration age on dung beetle taxonomic diversity (Fig. 2*A* and *SI Appendix, Fig. S5*). Sites with high plant phylogenetic diversity often had greater grass-relative abundance (*SI Appendix, Fig. S3*), which may explain observed decreases in dung beetle biodiversity because key resources are more difficult to locate. Meanwhile, soil conditions in older restorations might

provide a high-quality habitat for a wide range of fossorial species (100). Identifying such opposing responses to disturbance and succession may provide fertile ground to test hypotheses about the mechanisms structuring animal communities.

Quantifying the balance of these opposing management-driven and plant-driven effects may help resolve why restoration succeeds in some places but fails in others (53, 101, 102). Bivariate correlations between restoration approaches and measures of restoration success (e.g., biodiversity) can be deceptively simple, as these correlations reflect the net effect of many underlying ecological interactions (Fig. 2 and *SI Appendix, Figs. S5–S9*) (36, 42, 52). Small shifts in environmental context, such as interannual climatic variation, could alter the strength of plant-driven effects but not management-driven effects (or vice versa), leading to very different restoration outcomes (49). Predicting such context-dependent restoration outcomes might be possible with two key types of information. First, the network of all pathways contributing to biodiversity (e.g., management-driven effects versus plant-driven effects, Fig. 2) (87) must be identified. Second, the relative strength of important pathways must be quantified over key environmental gradients, such as climate and landscape connectivity (103). Identifying how the effects of restoration on complementary pathways vary over space and time will be critical for developing restoration ecology into a more mechanistic and predictive science.

Multiple Dimensions of Biodiversity May Be Needed to Capture Responses to Disturbance. Restoring biodiversity is essential for sustaining ecosystem function (52, 104), but it is often unclear which dimensions of biodiversity restoration efforts should be prioritized (105, 106). Because taxonomic diversity is agnostic about species identity, phylogenetic and functional diversity might provide a better indication of ecosystem recovery by describing the extent of ecological and evolutionary variation of species in restored ecosystems (19, 107, 108). In our study, management and restoration age had important effects on taxonomic and phylogenetic diversity of plants and animals and functional diversity of plants (Fig. 2 and *SI Appendix, Figs. S2 and S5*), suggesting that focusing solely on one dimension of biodiversity might miss important restoration outcomes. For example, sites with high plant phylogenetic diversity typically had more abundant grass species (*SI Appendix, Fig. S3*). These same sites also had a high relative abundance of phylogenetically unique small mammal species (Fig. 2), such as *Zapus hudsonius* (meadow jumping mouse), which is thought to predominantly consume grass seeds (109). Additionally, bison presence decreased dung beetle phylogenetic diversity (Fig. 2B and *SI Appendix, Fig. S5*), as sites with bison were dominated by *Onthophagus* species. However, maximizing phylogenetic diversity may not be an important restoration goal, especially if phylogenetic diversity is a poor predictor of functional diversity (110). Considering how restoration alters the phylogenetic and functional diversity of plant and animal communities may enable better integration of evolutionarily distinct species in restoration planning.

Incorporating multiple dimensions of animal biodiversity into restoration planning will require ecologists to continue developing

tools to quantify phylogenetic and functional diversity of animals. For example, phylogenies remain poorly described in many animal communities, making the ecosystem-wide consequences of animal phylogenetic diversity unclear (111). Similarly, functional traits for many animal taxa are rarely linked to ecosystem functions and often rely on coarse categorical variables that may miss important intra-specific or interspecific variation in function (112, 113). Technological advances, such as Global Positioning System tracking (114), stable isotope analysis (115), and DNA metabarcoding (116), may help identify functionally unique species or capture shifts in functional diversity in response to restoration (16). Ultimately, animal ecologists may be able to use phylogenies and functional traits to anticipate the effects of restoration on animal communities and resulting shifts in ecological function, similar to progress made in plant community restoration (117). By developing a deeper understanding of how animal biodiversity enhances ecosystem functioning (89, 98, 113), ecologists can help identify situations where restoring animal biodiversity should be a high priority.

Conclusions

Restoration shaped animal biodiversity primarily through pathways that were independent of changes in plant community biodiversity (Fig. 3), suggesting that the Field of Dreams hypothesis may fail to capture responses of many animal species to restoration. We observed this pattern in two vertebrate communities (small mammals and snakes) and two invertebrate communities (dung beetles and ground beetles), suggesting that this pattern may be observed in other animal groups (Fig. 2). While our structural equation models sorted ecological mechanisms into two broad categories to facilitate comparisons among a broad suite of organisms (management-driven and plant-driven effects), future research may develop more detailed models focusing on a single taxonomic group. For example, models could include changes in ecosystem function to explore how management-driven and plant-driven effects of restoration shape ecosystem services mediated by animals (43, 89). Alternatively, models might be extended to include interactions between different animal groups such as predation (3). By explicitly considering how restoration simultaneously shapes biodiversity at multiple trophic levels, ecologists can develop a more robust blueprint to restore Earth's degraded ecosystems.

Data Availability. Relative abundance and diversity data have been deposited in Dryad (<https://doi.org/10.5061/dryad.gflvhmnv>) (118).

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