

TOWARD PREDICTION IN THE RESTORATION OF BIODIVERSITY

Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration

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Summary

1. Recovering biological diversity and ecosystem functioning are primary objectives of ecological restoration, yet these outcomes are often unpredictable. Assessments based on functional traits may help with interpreting variability in both community composition and ecosystem functioning because of their mechanistic and generalizable nature. This promise remains poorly realized, however, because tests linking environmental conditions, functional traits, and ecosystem functioning in restoration are rare.

2. Here, we provide such a test through what is to our knowledge the first empirical application of the ‘response–effect trait framework’ to restoration. This framework provides a trait-based bridge between community assembly and ecosystem functioning by describing how species respond to environmental conditions based on traits and how the traits of species affect ecosystem functioning.

3. Our study took place across 29 prairies restored from former agricultural fields in southwestern Michigan. We considered how environmental conditions affect ecosystem functioning through and independently of measured functional traits. To do so, we paired field-collected trait data with data on plant community composition and measures of ecosystem functioning and used structural equation modelling to determine relationships between environmental conditions, community-weighted means of functional traits and ecosystem functioning.

4. Environmental conditions were predictive of trait composition. Sites restored directly from tillage (as opposed to those allowed to fallow) supported taller species with larger seeds and higher specific leaf area (SLA). Site age and fire frequency were both negatively related to SLA. We also found a positive relationship between soil moisture and SLA.

5. Both trait composition and environmental conditions predicted ecosystem functioning, but these relationships varied among the measured functions. Pollination mode (animal pollination) increased and fire frequency decreased floral resource availability, seed mass had a negative effect on

below-ground biomass production, and vegetative height increased decomposition rate. Soil moisture and fire frequency both increased while site age decreased above-ground biomass production, and site age and soil moisture both increased decomposition rate.

6. *Synthesis and applications.* Our results suggest that both trait composition and environmental conditions play a role in shaping ecosystem function during restoration, and the importance of each is dependent on the function of interest. Because of this, environmental heterogeneity will be necessary to promote multiple ecosystem functions across restored landscapes. A trait-based approach to restoration can aid interpretation of variable outcomes through insights into community assembly and ecosystem functioning.

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Introduction

Human land uses have modified a large proportion of natural ecosystems, causing a loss of biodiversity and alterations to the biological, geochemical, and physical processes that comprise the functioning of ecosystems (Foley *et al.* 2005; Cardinale *et al.* 2012; Haddad *et al.* 2015). In response, ecological restoration – active reinstatement of biological communities and ecosystem functionality – has been widely lauded for its potential to promote conservation success by increasing habitat area and quality (Dobson, Bradshaw & Baker 1997; Young 2000; Hobbs & Harris 2001; Brudvig 2011; Suding 2011). Yet, the notorious unpredictability of restoration outcomes challenges the potential success of restoration (Suding 2011). Promoting more predictable outcomes, in terms of biodiversity and ecosystem functioning, is a major goal of restoration ecology (Choi 2007; Rey Benayas *et al.* 2009; Matthews & Spyreas 2010). Considering the mechanisms by which communities assemble and thereby determine ecosystem functioning during restoration would provide insights into restoration outcomes, more predictable success, and transferability of findings among restoration efforts (Hobbs & Norton 1996; Palmer, Ambrose & Poff 1997; Brudvig 2011; Montoya, Rogers & Memmott 2012).

Functional trait-based approaches may be useful for understanding both community assembly and ecosystem functioning during restoration. Restoration ecology has typically focused on reinstating particular sets of species (Brudvig 2011) and this focus on taxonomic composition may limit generalization between restorations (Palmer, Ambrose & Poff 1997; Temperton 2004). Traits may provide insights into community assembly mechanisms to move beyond this idiosyncrasy. That is, a better understanding of how traits vary among species may predict how their dispersal, establishment, and persistence affect distribution and abundance among sites that vary in abiotic and biotic conditions (Weiher *et al.* 1999; McGill *et al.* 2006; Kraft, Valencia & Ackerly 2008). Species' functional traits are also related to ecosystem functioning (Díaz & Cabido 2001; Lavorel & Garnier 2002), and because of this, functional trait-based approaches may shed light on a second major goal of restoration: understanding the functioning of ecosystems and how this is related to the diversity and composition of communities (Tilman, Isbell & Cowles 2014). Thus, functional traits hold great promise for interpreting, predicting, and linking the assembly and functioning of communities and ecosystems.

The 'response–effect trait framework' integrates functional traits and restoration by incorporating two

ideas: (i) community assembly is mediated by how functional traits respond to environmental conditions (response traits), and (ii) ecosystem functioning is influenced by the trait composition of the community (effect traits) (Lavorel & Garnier 2002; Suding *et al.* 2008). Response and effect traits may be independent, correlated to one another, or one-and-the-same (i.e. the same trait responds to environmental conditions and determines function), depending on the assembly mechanism and function of interest (Lavorel & Garnier 2002). Correlations between traits have often been considered at the level of the individual in the context of life-history trade-offs (Westoby 1998; Weiher *et al.* 1999), but traits may also be correlated at the community level if suites of species possessing similar functional traits respond to the same assembly processes. For example, plant height and specific leaf area (SLA) may be uncorrelated within species, but if both traits respond to a site level factor, such as nutrient availability, there may be a correlation in site level averages of these traits. Understanding the correlations or trade-offs among functional traits at both within-species and community levels is important for linking the processes that determine composition and function. Finally, site-to-site variation in environmental conditions – either modified by or independent of restoration actions – might also affect ecosystem functioning through processes not mediated by functional traits (Fig. 1). In spite of its promise for interpreting restoration outcomes and linking environmental conditions (including those manipulated through restoration), community assembly, and ecosystem functioning

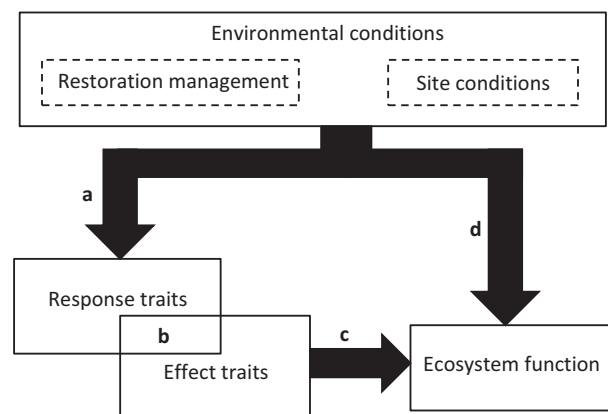


Fig. 1. Conceptual diagram illustrating: (a) community assembly, the processes by which environmental conditions (both site conditions and restoration management) determine response trait composition. (b) The possible relationship between response and effect traits. (c) The process by which effect traits produce ecosystem function. (d) The independent effect of environmental conditions on ecosystem function, not mediated by functional traits.

(Perring *et al.* 2015), no tests, to our knowledge, have evaluated the response–effect trait framework in restoration. Instead, restoration ecology has generally focused on how environmental conditions determine species composition or diversity and diversity–ecosystem function relationships independently (Montoya, Rogers & Memmott 2012).

Here, we evaluate the trait response–effect framework within tallgrass prairies in southwestern Michigan, which have been restored by sowing native prairie seeds onto former agricultural lands. We employ structural equation modelling (SEM; Grace 2006) to consider the relationships among site conditions and actions taken during restoration, plant functional trait composition, and aspects of ecosystem functioning within these sites. We address three questions: (i) In what ways do environmental conditions affect plant functional trait composition? (ii) What are the relationships between environmental conditions and ecosystem functioning and how are these mediated through plant functional traits? (iii) Are response and effect traits correlated, uncorrelated, or one-and-the-same, and what insights do these relationships provide for interpreting the response–effect trait framework?

Materials and methods

STUDY SYSTEM

We addressed these questions within a set of 29 tallgrass prairies in southwestern Michigan, restored from former agricultural fields through seed sowing. Tallgrass prairie was once a dominant ecosystem across much of central North America, but this area has been reduced to less than 0.1% due to conversion to agriculture and other human land uses (Samson & Knopf 1994). Today, tallgrass prairie restorations are typically initiated through sowing seeds of native prairie plants onto former agricultural lands and, subsequently, the resulting grasslands are managed with prescribed fire and other approaches (Packard & Mutel 1997).

The 29 sites were located across four counties and ranged in size from <1 to >38 ha and were 5–9 years old at the time of sampling. Sites were managed with prescribed fire and were burned 0–4 times. We expected fire to affect plant communities through species' traits by promoting species with fire adaptations, such as having low SLA to conserve nutrients (Cornelissen *et al.* 2003; Cavender-Bares & Reich 2012). Sites varied in their land-use history. After cessation of row-crop agriculture, some sites were immediately restored, while others were managed for hay, or allowed to fallow for one or more years before being restored. Previous land use influences plant community composition (Grman, Bassett & Brudvig 2013) and likely alters trait composition. The landscape surrounding each site also varied. We analyzed the surrounding landscape using ArcGIS, to calculate the total amount of the landscape covered by forest, grassland, wetland, agriculture, or urban area within a 500m radius (9.3.1, ESRI 2009, Redlands, CA, USA; Grman, Bassett & Brudvig 2014). The surrounding landscape can influence composition of the plant community based on which species are able to disperse from different landscape types and through trophic interactions.

FIELD DATA COLLECTION

We determined plant species composition and abundance (% cover) within 10 1 × 1 m plots at each site along a 45 m transect during August 2013. We took eight 3 cm² by 20 cm deep soil cores around each plot and combined them to form a composite sample for each site which we analyzed for soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, and pH (Brookside Laboratories, New Knoxville, OH, USA). Separately, we assessed soil water holding capacity at the plot level by calculating the proportion of oven dried weight to saturated wet weight and used site means for analysis (Brudvig & Damschen 2011). We expected these soil components to influence trait composition based on species nutrient uptake strategies and drought stress capabilities.

We also measured six ecosystem functions at each site: above-ground biomass production, belowground biomass production, decomposition rate, floral resource availability, and two aspects of trophic dynamics: seed predation and arthropod predation. We measured aboveground biomass production by clipping all plant material at the end of the 2013 growing season in each 1 × 1 m plot. We sorted samples to remove litter and oven dried at 65 °C for at least 48 h before weighing. To measure belowground biomass, we took 3 cm² by 20 cm deep soil cores from the corner of each plot at the end of the growing season. We passed soil cores through a 2 mm sieve to collect all roots which were then washed and dried at 65 °C for 48 h before weighing. We measured decomposition rate adjacent to each 1 × 1 m plot by placing 3.80 ± 0.01 g of cellulosic fibre paper inside a sealed 15.5 × 15.5 cm mesh bag (mesh size 2 mm²) at the soil surface, beneath the litter layer. We collected mesh bags after 108–123 days and dried at 65 °C for 48 h before weighing. We calculated decomposition rate by subtracting final mass from starting mass and dividing by the time they remained in the field. We measured floral resource availability by estimating the percent cover of showy flowers likely pollinated by animals within each 1 × 1 m plot in June, July, and September 2013. We calculated total floral cover by summing across all three sampling periods. We measured seed predation, which can have important bearing on seedling recruitment during restoration (Germain *et al.* 2013), by placing 20 seeds per species for each of four prairie species common across our sites (*Sorghastrum nutans*, *Desmodium canadense*, *Monarda fistulosa*, and *Rudbeckia hirta*) within 12 × 12 × 5.5 cm plastic containers with two 6.5 × 4.5 cm openings cut from adjacent sides of each container to allow access to arthropod and mammalian seed predators. Because we covered containers to prevent seed loss during rainstorms, this design excluded birds that may also function as seed predators in this system (Howe & Brown 1999). We placed seeds on a small amount of sand within each container to mimic soil surface conditions. We placed one container at ground level adjacent to each plot and collected after 13 days. We calculated seed predation rate as the total number of seeds removed from each trap. Finally, we measured arthropod predation rate by securing four wax worms (*Galleria mellonella*) to a Petri dish and then covering worms with a small amount of sand to reduce desiccation but allow visibility. We placed the Petri dishes at ground level adjacent to each plot and covered them with a wire cage, with 1.27 cm wide holes, to prevent predation from birds and mammals, owing to concerns of uniformly high predation. After 24 h we counted the number of wax worms removed from each plate by arthropod predators.

TRAIT COLLECTION

We collected trait data for species that were present during surveys using standard methods (Pérez-Harguindeguy *et al.* 2013). We focused on four traits – vegetative height, pollination mode, SLA, and seed mass – because these are thought to affect community assembly through the processes of dispersal, establishment, and persistence and/or are related to the functions we quantified (Weiher *et al.* 1999; Díaz & Cabido 2001). We obtained most trait data from individuals at one of our 29 sites. While we recognize the important role that intraspecific trait variation can play in community assembly (Jung *et al.* 2010; Laughlin *et al.* 2012), it was infeasible to meaningfully quantify intraspecific variation across the 170 species in our dataset. We collected traits from haphazardly-selected healthy, flowering adults in full sun (Cornelissen *et al.* 2003), located at least 10 m away from a site edge. Vegetative height is related to a species' competitive ability with taller species better adapted to compete for light (Weiher *et al.* 1999). We measured vegetative height as the distance between the ground and highest photosynthetic structure on 20 individuals. SLA is also related to competitive ability, as species with low SLA are better competitors for limiting resources such as nitrogen (Weiher *et al.* 1999). SLA also relates to growth rate and stress tolerance with faster growing and less stress tolerant species having higher SLA (Wright *et al.* 2004). We measured SLA by collecting two leaves from each of 10 individuals. We kept leaves turgid and stored on ice for <10 h until area was determined with a leaf area scanner. We then dried leaves at 65 °C for 48 h before weighing. We calculated SLA as leaf area divided by dry mass. Seed mass is related to dispersal and establishment, with smaller-seeded species producing more seeds per reproductive effort, increasing the chance of dispersal; while species with larger seeds are more likely to establish in competitive environments (Westoby 1998). Smaller seeded species are also more likely to form persistent seed banks (Thompson & Grime 1979) allowing them to establish after disturbance. We determined seed mass by taking the average of at least 50 seeds for each species dried at 80 °C for 48 h before weighing. When necessary, we supplemented seed mass data from the KEW seed information database (Royal Botanic Gardens Kew, 2016). Pollination mode is related to whether or not a species produces flowers meant to attract pollinators. We determined pollination mode by classifying whether or not each species produces showy flowers likely to be attractive to pollinators. Because trait data were missing only for some uncommon species and our trait analyses were weighted by species abundances (see below), missing trait data likely had little impact on our results. In sum, across traits, we acquired vegetative height and SLA trait data for species representing 90% of abundance in our surveys and pollination mode on 100% of species; we collected 78% of seed mass data in the field and 17% from Kew (95% total).

ANALYSIS

We conducted analyses in R v.3.0.2 (R Core Team 2013). We first calculated community weighted means (CWM) for each functional trait at each site. We did this by weighting the trait value of each species by its total percent cover at each site (summed across plots) to calculate a mean value for each trait at each site. Because of correlations among soil variables and among landscape context variables (Grman, Bassett & Brudvig 2013), we used principle components analysis (PCA) to create one variable describing soil conditions and one describing landscape context.

The soil PCA included soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, pH, and water holding capacity. The first PC axis described 56% of variation in soil variables and was positively related to silt, clay, soil organic matter, pH, and water holding capacity and negatively related to sand and both measures of phosphorus. The landscape context PCA included the total amount of land covered by agriculture, forest, wetland, grassland, or development. The first PC axis described 59% of variation in landscape variables and was positively related to forest, grassland, and wetland cover and negatively related to agriculture and development. Finally, we logit transformed the floral resource availability variable to meet normality assumptions (Warton & Hui 2011).

We then developed SEMs using the Lavaan package in R (Rosseel 2012) based on hypothesized relationships between environmental conditions, functional traits and ecosystem functions (see Appendix S1, Supporting Information). SEM is a useful tool for understanding the direct and indirect effects of predictors in complex multivariate systems (Grace *et al.* 2012). To test question 1 and determine how traits responded to the environmental conditions, we predicted CWM trait values for vegetative height, SLA, and seed mass with site age, soil moisture (first soil PC axis), fire return interval, landscape context (first landscape PC axis) and land-use history. To test question 2 we predicted each ecosystem function based on CWM traits and the environmental conditions, using a separate model for each ecosystem function: aboveground biomass production, belowground biomass production, decomposition rate, floral resource availability, seed predation rates, and arthropod predation rates. We allowed all environmental conditions to covary with each other, and we also allowed all CWM trait means to covary with one another. We expected these covariances because of un-modelled common causes (i.e. environmental conditions within the same site or functional traits on the same species). We examined modification indices to determine whether there were paths missing from the models that significantly improved model fit based on the single-degree-of-freedom chi-square criterion of 3.84 (equivalent to $P < 0.05$) (Grace 2006). We added paths that met this criterion and were biologically plausible. We tested for deviation from multivariate normality using the psych package in R (Revelle 2016). Only floral resource availability had significant kurtosis. For this model we calculated Sartorra–Bentler adjusted χ^2 . All SEM meta-models are shown in Figs S1–S6.

To test question 3 and address possible correlations among response and effect traits, we used the Hmisc package in R to test for significant Pearson's correlations between all pairwise CWM trait values and all functional traits at the species level (Harrell 2004).

Results

The SEMs fit the data well (minimum $P = 0.40$ for χ^2 goodness of fit; $P > 0.05$ indicates good fit; Grace 2006) and accounted for differing amounts of variation in ecosystem function ($R^2 = 0.09$ – 0.46). All path coefficients reported below (r) have been standardized, so their values can be compared to assess their relative effect sizes.

COMMUNITY ASSEMBLY

Structural equation modelling for each of the six ecosystem functions had the same community assembly paths;

i.e. those between environmental conditions and trait CWMs (Fig. 2). Only land-use history explained variation in CWM seed mass ($R^2 = 0.17$), where seed mass was higher on sites that were restored directly from tillage ($P = 0.03$, $r = 0.39$). Similarly, only land-use history explained vegetative height ($R^2 = 0.23$), with higher values on sites restored directly from tillage ($P = 0.01$, $r = 0.45$). Vegetative height was slightly higher on sites with higher soil moisture, but this relationship was only marginally significant ($P = 0.064$, $r = 0.25$). Finally, SLA was explained by fire frequency, land-use history, site age, and soil moisture ($R^2 = 0.42$). Older sites or those that burned more frequently had species with lower SLA ($P = 0.02$, $r = -0.34$; $P = 0.02$, $r = -0.37$). Sites restored directly from tillage contained species with higher SLA ($P = 0.002$, $r = 0.49$). Drier sites had species with higher SLA ($P = 0.04$, $r = 0.30$).

ECOSYSTEM FUNCTIONING

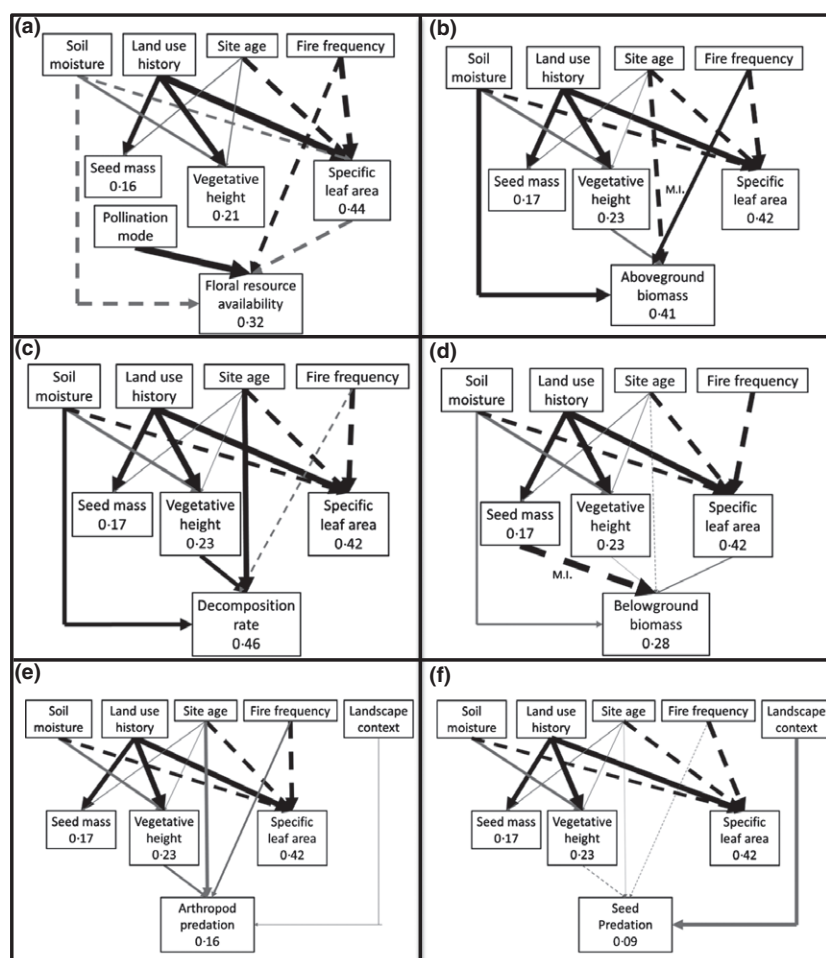
Environmental conditions influenced ecosystem functioning, both directly and indirectly through their influence on traits. Below we report the total standardized effect (TSE) or the sum of all direct and indirect standardized path coefficients between a predictor and response variable.

Subsequently, we report the proportion of the TSE explained by the direct relationship between environmental conditions and each ecosystem function and the proportion mediated by functional traits.

Floral resources were influenced by trait composition and environmental conditions (Fig. 2a, $R^2 = 0.32$). Communities supporting more animal-pollinated species produced more floral resources ($P = 0.002$, $r = 0.53$). There was a negative TSE of fire frequency on floral resource availability (Fig. 3, TSE = -0.19). This effect was largely driven by a direct negative effect of fire on floral resources ($P = 0.05$, $r = -0.31$). There was also a negative TSE of soil moisture on floral resource availability (TSE = -0.2), largely due to a marginally significant direct effect of soil moisture on floral resource availability as drier sites had higher floral resource availability ($P = 0.08$, $r = -0.29$).

Aboveground biomass production was influenced by environmental conditions, but not traits (Fig. 2b, $R^2 = 0.41$). There was a positive effect of fire frequency on biomass production (Fig. 3, TSE = 0.29), largely due to a direct positive effect of fire on biomass production ($P = 0.04$, $r = 0.29$). There was also a positive TSE of soil moisture on biomass production (TSE = 0.44), resulting from a direct effect of soil moisture on biomass production. Aboveground biomass was greater on wetter sites

Fig. 2. Structural equation models for each ecosystem function. Each panel (a–f) represents a different ecosystem function. Reasoning for each path is listed in Appendix S3. Black paths represent significant relationships ($P < 0.05$). Grey paths represent non-significant relationships. Paths labelled M.I. show relationships added based on suggestions from modification indices. Solid lines represent positive relationships and dashed lines negative relationships. Paths are weighted by standardized path coefficients. Values inside of the box are the R^2 values for that response variable. All environmental conditions covary with one another as do all CWM trait values (not shown). Meta-models for each SEM are shown in Figs S1–S6.



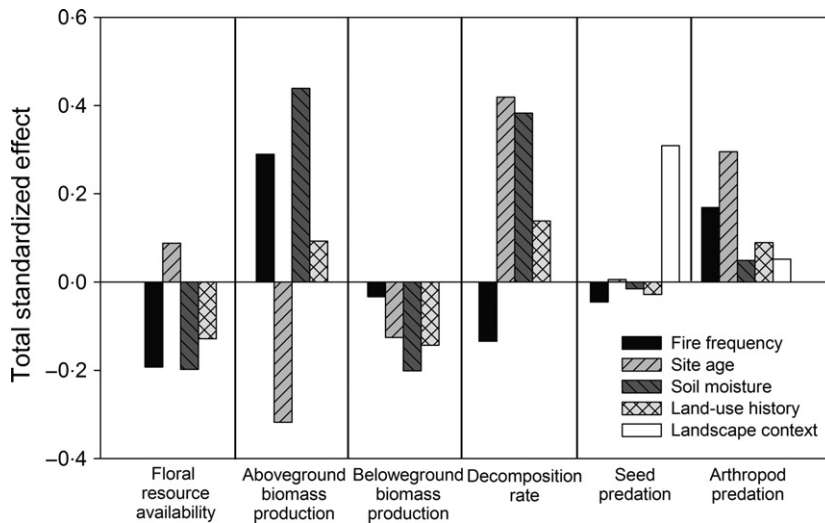


Fig. 3. Total standardized effect of each environmental condition on each ecosystem function. Landscape context was only included in the seed predation and arthropod predation models.

($P = 0.01$, $r = 0.39$). Modification indices suggested including a path between site age and biomass; the negative effect (TSE = -0.32) was due to a direct relationship where older sites produced less aboveground biomass ($P = 0.025$; $r = -0.33$).

Belowground biomass production was influenced by trait composition, but not directly by environmental conditions (Fig. 2c, $R^2 = 0.28$). A negative effect of land-use history on belowground biomass (Fig. 3, TSE = -0.14) was largely related to a small indirect effect with sites being restored directly from tillage having higher seed mass and in turn less belowground biomass ($P = 0.02$, $r = -0.50$). Modification indices suggested including the path between seed mass and belowground biomass. This path is likely due to seed mass being correlated with an unmeasured trait that influences belowground biomass.

Decomposition rate was influenced by both trait composition and environmental conditions (Fig. 2d, $R^2 = 0.44$). Decomposition rate increased with site age (Fig. 3, TSE = 0.42) because of a direct effect, with older sites having higher decomposition rates ($P = 0.004$, $r = 0.40$). Decomposition also increased with soil moisture (TSE = 0.38) because of a direct effect, where wetter sites had higher decomposition ($P = 0.03$, $r = 0.31$), and an indirect effect, where wetter sites had taller species and decomposition rate was faster within taller communities ($P = 0.03$, $r = 0.31$).

Arthropod predation was not influenced by trait composition or environmental conditions (no significant relationships; Fig. 2e, $R^2 = 0.16$). However, arthropod predation did increase with site age (Fig. 3, TSE = 0.30) because of a marginally-significant ($P = 0.1$) direct effect where older sites had more predation ($r = 0.29$).

Seed predation rate was weakly influenced by environmental conditions (Fig. 2f, $R^2 = 0.09$), but we found no evidence for an influence of trait composition. Seed predation varied

with landscape context (Fig. 3, TSE = 0.31) because of a marginally-significant ($P = 0.09$) direct effect. Sites surrounded by forest and grasslands had higher seed predation rates than sites surrounded by developed and agricultural areas ($r = 0.31$).

TRAIT CORRELATIONS

We found varying degrees of correlation between CWM trait values across our sites (Fig. 4). Sites with more cover of tall species had less cover of animal-pollinated species ($r = -0.40$, $P = 0.03$) and greater seed mass ($r = 0.65$, $P = 0.0001$). Sites with more animal-pollinated species had higher SLA ($r = 0.41$, $P = 0.03$). We found that correlations between traits occurred primarily because of community level processes at our sites and not because of correlations among traits at the species level, as we found no significant correlations between traits at the species level (Fig. S7).

Discussion

Understanding how ecological communities assemble and how species assemblages determine ecosystem functioning are major goals of ecology broadly and restoration ecology specifically. Here, we provide what is, to our knowledge, the first application of the response–effect trait framework to restoration, integrating these two concepts (Lavorel & Garnier 2002). Ecological theory suggests that interpreting restoration through the lens of trait-based approaches to community assembly (Weiher *et al.* 2011) and ecosystem functioning (Díaz and Cabido 2001) will confer greater predictability and more generalizable outcomes (Suding *et al.* 2008). Real-world tests of these ideas are important but rare (Cardinale *et al.* 2012). By providing such a test, our work leads to four key insights. First, by applying a trait response–effect framework, we show the relationships among environmental conditions, plant

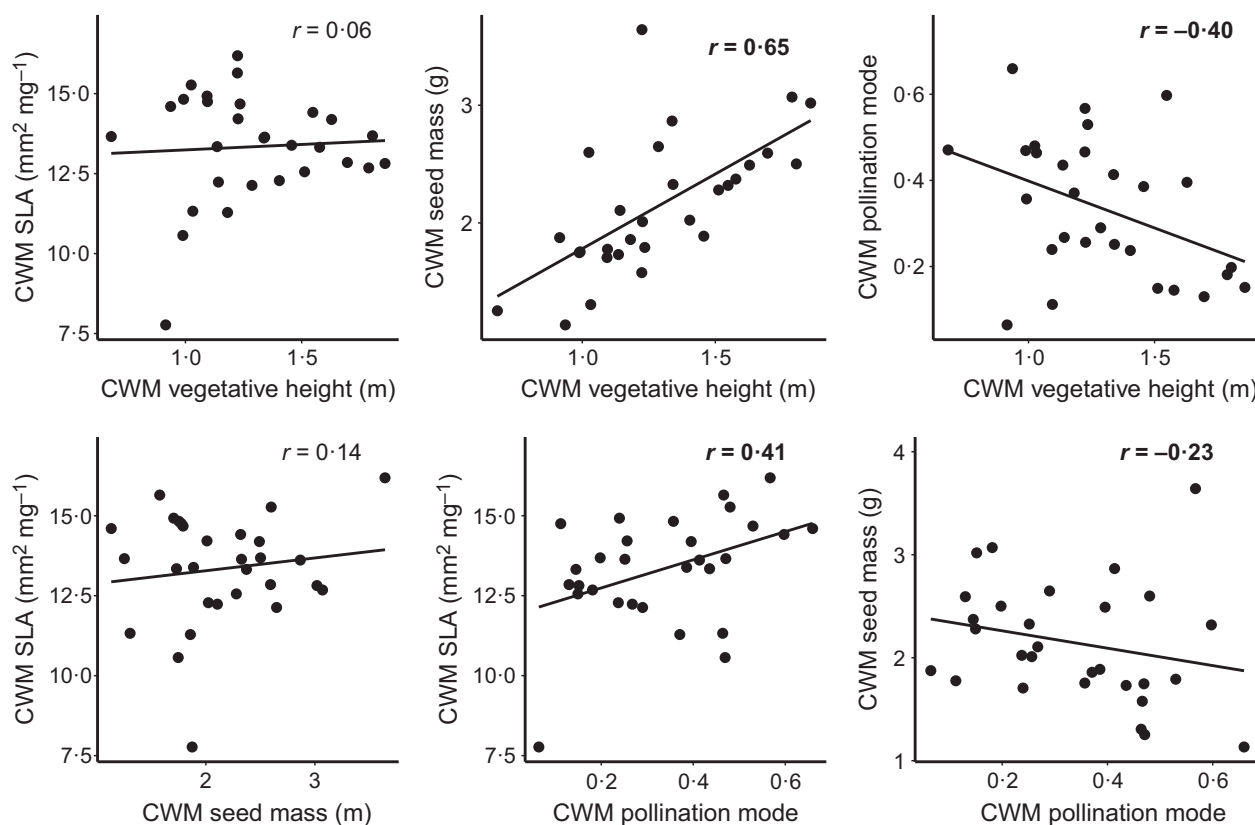


Fig. 4. Bivariate correlations between all pairwise CWM traits. Bolded r values represent significant Pearson's correlations ($P < 0.05$). Each point represents a study site. Plots of species level trait correlations are shown in Fig. S7.

functional traits, and ecosystem functioning. Second, prairie communities assembled based on how traits responded to environmental conditions, including those influenced by restoration. Third, traits and environmental conditions together influenced ecosystem functioning, yet these relationships varied among functions and no one environmental condition or set of traits impacted all functions. Finally, we illustrated how functional traits are correlated across sites, which may have important implications for connecting community assembly and the provisioning of ecosystem function. Together, these results demonstrate the utility of applying the response–effect framework to restoration.

Our models did a good job of explaining community assembly, relating environmental conditions to trait composition across sites, and providing insights into mechanisms of assembly. For example, sites that were burned more frequently supported a community with lower SLA, likely because fire clears litter and volatilizes nutrients which reduced competition for light and increased nutrient competition (Knapp & Seastedt 1986; Cavender-Bares & Reich 2012). Species with lower SLA are considered worse light competitors but may be better competitors for limiting soil nutrients (Grime 1977; Westoby 1998). Additionally, land-use history – whether or not a site was allowed to fallow following tillage agriculture – predicted vegetative height, SLA, and seed mass. Previous land use

can affect the composition of weedy species, and potentially residual soil nutrient levels, during prairie restoration from agriculture (Grman, Bassett & Brudvig 2013). We found that sites restored directly from tillage, rather than being allowed to fallow, contained taller species with larger seeds and higher SLA. This suggests that shorter, low SLA weedy species may be important drivers of trait composition during prairie restoration either through their establishment or how they affect the establishment of other species through competition. If land-use legacy, fire disturbance, and other mechanisms of community assembly are generalizable through traits (Laughlin 2014), our community assembly findings have important bearing on how sites are selected for restoration, subsequent management decisions, and predicting restoration outcomes more broadly.

We also showed that ecosystem functions responded to both environmental conditions and traits and that no single environment or plant community maximized all functions. Consequently, variability in environmental conditions and management practices will be necessary to promote multiple ecosystem functions across a restored landscape. For example, sites with low soil moisture supported higher levels of floral resources and belowground production, but lower levels of aboveground production and decomposition (Fig. 3). As a result, maximizing levels of these functions will require restoring areas with both

high and low soil moisture. Other studies have also shown that heterogeneous landscapes lead to variable levels of multiple ecosystem functions across a landscape (Lavorel *et al.* 2011). We recognize that the use of standardized materials across sites may have affected the relationships we observed between functional traits and this ecosystem function. For example, we observed no relationship between SLA and decomposition, yet use of site-specific leaf material might have yielded a relationship between high SLA leaf litter and high decomposition rates (Garnier *et al.* 2004). We recognize that our ability to explain variation in ecosystem functioning ranged widely ($R^2 = 0.09\text{--}0.46$), and was often independent of core traits used in community ecology, suggesting the need for better models (e.g. more robust trait or environmental data). Alternatively, there may be inherent variation in predictability among functions. Both non-mutually exclusive possibilities suggest the need for more tests of how traits and environmental conditions affect ecosystem functioning among sites during restoration.

Our results illustrate the utility of the response–effect trait framework by showing how the relationships between response and effect traits are important for linking environmental conditions to levels of ecosystem functions and the processes of community assembly and ecosystem functioning. We showed that this is because response and effect traits can be the same trait, traits that are correlated with one another, or uncorrelated and that this is dependent on the environmental conditions, functional traits, and ecosystem functions being measured. One example of response and effect traits being one-and-the-same in our system is vegetative height, which responded to land-use history and affected decomposition rate. There were also situations where a trait affected ecosystem function, was not directly influenced by environmental conditions, but correlated with one or more other traits that did respond to environmental conditions. For example, although land-use history did not affect pollination mode or floral resources directly, it may have done so indirectly via the correlation between pollination mode and vegetative height. The correlation between pollination mode and vegetative height is not a species-level trade-off with shorter species producing animal pollinated flowers (Fig. S7) but instead a site-level trade-off (Fig. 4). One potential explanation is that vegetative height increases with C4 grass abundance, which also causes a reduction in animal pollinated species (Fig. S8). Dominance of C4 grasses during prairie restoration has been shown to cause strong competition for resources and the loss of forb species (Dickson & Busby 2009). Correlations between response and effect traits are important for understanding how the assembly process can indirectly influence ecosystem functioning. Situations where response and effect traits are one-and-the-same or correlated confer predictability based on relationships between assembly and functioning. In these instances, restoration practitioners may be able to choose sites with certain environmental conditions or use management techniques to alter these

conditions to promote ecosystem functions of interest. However, response and effect traits can also be uncorrelated, which could limit our ability to predict functioning. For instance, we detected no effect traits that predicted seed predation, and modification indices did not suggest any other trait associations with seed predation that could be correlated with unmeasured effect traits. In such cases, we may be unable to predict levels of function based on commonly measured functional traits or the assembly mechanisms to which traits respond. It will be important for future work to determine correlations between traits that respond to environmental conditions and have an effect on ecosystem function.

Despite these complications, our results illustrate the value of the response–effect trait framework for conducting restoration. Our work informs decisions about restoration site selection and management practices within sites undergoing restoration. Certain site conditions, such as soil moisture and landscape context, cannot be easily manipulated but can have large impacts on trait composition and ecosystem functioning. Within our sites, drier sites contained species with higher SLA. These sites also produced higher floral resources but lower levels of aboveground biomass and had lower decomposition rates (Fig. 3). We also found that sites surrounded by forests and grasslands had higher seed predation rates than those surrounded by agriculture and development. In these situations, decisions about which sites to restore will be important if we have particular composition or function goals. Other environmental conditions, such as fire frequency, are also important for trait composition and ecosystem functioning and can be directly manipulated during restoration. Prescribed fire is a powerful restoration tool for shaping species composition and functioning, such as aboveground biomass production (Briggs & Knapp 1995; Spasojevic *et al.* 2010). Our results suggest an important mechanism for this process, by which increasing fire frequency decreases SLA across our sites. Increased fire frequency also alters the provisioning of ecosystem functions across our sites, decreasing floral resources and increasing aboveground biomass production (Fig. 3). Our results also suggest that actions taken to compensate for land-use history (such as depleting a weedy seed bank) can have major implications for trait composition and ecosystem function. Our results show that fallowing prior to restoration resulted in markedly different trait composition with lower vegetative height, SLA, and seed mass, compared to sites restored directly from tillage. This change in trait composition impacted function, with fallowed sites having more floral resources and belowground biomass but less aboveground biomass and lower rates of decomposition. Future work should consider additional functional traits that might influence community assembly and ecosystem functioning during restoration. For example, root traits, such as specific root length or rooting depth, might influence functions such as belowground biomass production.

There is a strong pragmatic need to apply ecological theory to restoration, to increase predictability and

decrease idiosyncrasy between restorations (Palmer, Ambrose & Poff 1997; Young, Chase & Huddleston 2001; Choi 2007). Our results provide an important empirical bridge between the theory and applied utility of functional traits for interpreting how individuals respond to environmental conditions, affect interactions within and between trophic levels, and influence the ways that ecosystems function during restoration (Weiher *et al.* 1999; Lavorel *et al.* 2013; Kraft, Godoy & Levine 2015). In turn, our work illustrates the utility of restored ecosystems for testing theory in trait-based ecology because they inherently manipulate assembly (e.g. through seed sowing) and environmental conditions that modify assembly (e.g. prescribed fire). In doing so, we illustrate how understanding relationships between environmental conditions, functional traits and ecosystem functions can guide restoration practice to meet composition and ecosystem function goals within a restored landscape.

Authors' contributions

All authors contributed to data collection, the ideas in the manuscript, and to revising drafts of the manuscript. C.Z. analyzed data and wrote the first draft of the manuscript.

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Data accessibility

Data and R code available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2175q> (Zirbel *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Figs S1–S6. Meta-models representing the relationships between environmental conditions, functional traits, and each ecosystem function.

Appendix S2. Figs S7 and S8. Figure S7 shows the bivariate correlations between all pairwise traits at the species level. Figure S8 shows the relationships between sown C4 grass abundance and CWM vegetative height and CWM pollination mode at each site.

Appendix S3. Theoretical basis for the hypothesized relationships in the structural equation models.