



Testing the hypothesis of hierarchical predictability in ecological restoration and succession

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Received: 11 February 2017 / Accepted: 5 December 2017
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Abstract

To advance predictive ecology, the hypothesis of hierarchical predictability proposes that community measures for which species are interchangeable (e.g., structure and species richness) are more predictable than measures for which species identity matters (e.g., community composition). Predictability is hypothesized to decrease for response measures in order of the following categories: structure, species richness, function, and species composition. We tested this hypothesis using a 14-year, oak savanna–prairie restoration experiment that removed non-native pine plantations at 24 sites in northwestern Ohio, USA. Based on 24 response measures, the data showed minimal support for the hypothesis, because response measures varied in predictability within categories. Half of response measures had over half their variability modeled using fixed (restoration treatment and year) and random plot effects, and these “predictable” measures occurred in all four categories. Pine basal area, environment (e.g., soil texture), and antecedent vegetation accounted for over half the variation in change within the first three post-restoration years for 77% of response measures. Change between the 3rd and 14th years was less predictable, but most restoration measures increased favorably via sites achieving them in unique ways. We propose that variation will not conform with the hypothesis of hierarchical predictability in ecosystems with vegetation dynamics driven by stochastic processes such as seed dispersal, or where vegetation structure and species richness are influenced by species composition. The ability to predict a community measure may be more driven by the number of combinations of casual factors affecting a measure than by the number of values it can have.

Keywords Oak savanna · Plantation · Site variability · Variance partitioning · Vegetation change

Introduction

Predicting changes in ecosystems has been a goal of ecology since the inception of ecological science. The study of succession, for example, one of ecology’s oldest topics of study,

seeks to model and forecast short- and long-term vegetation dynamics. Similarly, a goal of restoration ecology, which pursues understanding how to repair damaged ecosystems, is predicting ways vegetation changes during restoration. Many ecologists have noted that studying ecosystem dynamics during ecological restoration has potential for generating new insight into topics long of general interest in ecology such as succession, community assembly, and predictive ecology (e.g., Bradshaw 1983; Palmer et al. 1997; Walker et al. 2007).

Recently, Brudvig et al. (2017) proposed a hierarchy of predictability hypothesis that could apply to ecological restoration, succession, and community ecology. This hypothesis proposes that predictability of restoration outcomes is highest for vegetation response measures that have few possible outcomes and for which species are functionally redundant. Predictability is least for response measures with many possible permutations where species identities matter. For example, a community’s species composition

Communicated by Catherine Gehring.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-017-4040-z>) contains supplementary material, which is available to authorized users.

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(species present and their relative abundance) can result from countless combinations of species and abundances for all but the simplest communities, potentially making species composition highly variable and difficult to predict. On the other hand, species are interchangeable for a measure such as species richness, meaning that numerous combinations of species could result in identical species richness. Similarly, vegetation structure, such as whether a forest developed (e.g., defined as a site containing trees over a certain height), potentially has fewer possible outcomes than tree species composition for any forest containing more than one tree species, because multiple tree species could be functionally redundant at meeting the height criteria. This reasoning builds upon ideas previously suggested by succession, where succession ecologists have hypothesized that measures for which species are interchangeable (e.g., cover by growth form groups such as herbaceous versus woody plants) shift more predictably during succession than does species composition (e.g., Prach and Walker 2011; Meiners et al. 2015). The hierarchy of predictability hypothesis, formalized by Brudvig et al. (2017), posits that predictability is highest to lowest in the following order: (i) vegetation structure (e.g., total biomass or cover); (ii) species richness; (iii) functional measures (e.g., abundance of flowering forbs); and (iv) species composition.

Important in both restoration and succession ecology, and with implications for evaluating the hierarchy of predictability hypothesis, is distinguishing between the “average” change or difference and the variation in response among sites. In other words, conditions may differ on average between restoration and control treatments (or among, say, disturbance types in unmanipulated succession), but this could result from just a portion of sites favorably responding to restoration, while the remaining sites perhaps do not even differ from controls. As a result of this scenario, the aggregate outcome of restoration (i.e., restoration and control treatments differ on average) might be more predictable for most response measures than the restoration outcomes at individual restoration sites. One way to evaluate how much variability in a response measure is attributable to restoration treatments, as compared to site effects, is variance partitioning (e.g., Norden et al. 2015; Laughlin et al. 2017). For example, if restoration treatment accounts for most variation in a response measure, restoration outcomes may be predictable. However, if random site effects account for more variance than treatment, restoration outcomes may be unpredictable.

We used a Midwestern USA oak savanna–prairie restoration as a model system to evaluate the following questions: (1) how have a range of vegetation structure, species richness, functional, and species composition measures varied during restoration? (2) what were the relative contributions of restoration treatment, time, soils, and prior vegetation

to variability in vegetation changes? and (3) how well do results match the hierarchy of predictability hypothesis?

Materials and methods

Study area

Our study area was within the Midwestern savanna region of North America, supporting landscapes with mixtures of oak (*Quercus*) savanna, woodland, and prairie that are among the continent’s most high-priority ecosystems for restoration (Schetter and Root 2011). These fire-dependent communities were estimated to cover over 12 million ha in the early 1800s, before Euro-American settlement initiated clearing for agriculture, wood cutting, livestock grazing, hydrological alteration, urban–suburban development, and suppressing frequent fire (Nuzzo 1986). These changes eliminated the habitats or converted them to closed-canopy forest, reducing savanna by > 99% between pre-settlement and the 1980s (Nuzzo 1986).

In an eastern part of the Midwestern savanna landscape, we performed our experiment in northwestern Ohio, USA, within the 45,000-ha Oak Openings region (Fig. 1). Climate is temperate with warm summers and cold winters, and averages of 85 cm of annual and 34 cm of growing season (May through August) precipitation (Online Resource 1). Based on 1817–1832 U.S. Government General Land Office surveys, this sandy region at that time contained a mixture of oak woodland, savanna, and wet prairie (Brewer and Vankat 2004). Our study area was the 1497-ha Oak Openings Preserve (41°33′N, 83°51′W), the largest protected area in the region, and managed by the Metroparks of the Toledo Area. When the initial lands for the preserve were acquired in the 1930s, much of the area was abandoned agricultural land. To revegetate these lands, managers established plantations of pines—primarily *Pinus strobus* and *resinosa*—native to North America but not to the Oak Openings region (Moseley 1928). It was intended to periodically thin the plantations, but this did not occur, because timber markets and management priorities changed. By the early 2000s, interest heightened in replacing plantations with native vegetation, owing to minimal diversity in the plantations, unhealthy status of conifer trees in the overstocked plantations, and an opportunity to restore globally imperiled native ecosystems. The ecological restoration goals included creating open-structured, oak–prairie ecosystems, plus increasing native plant cover, species richness, conservation-priority rare plants, floristic quality toward more natural savannas–prairies, wetland plants characteristic of natural upland–wetland biophysical gradients, and flowering plants for invertebrates and pollinators.

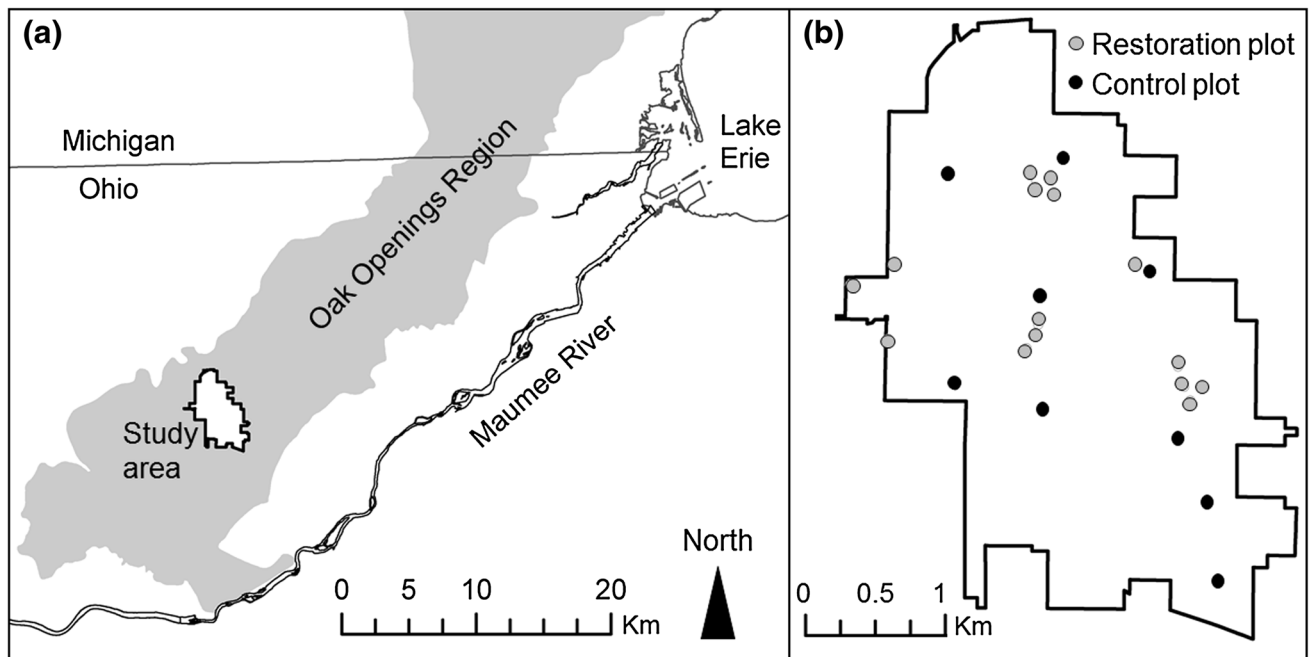


Fig. 1 Location of the **a** Oak Openings region in northwestern Ohio, USA, and **b** distribution of plots in the Oak Openings Preserve study area. Restoration plots were spatially clustered to encompass approxi-

mately equal numbers of plantations by pine species, but no spatial autocorrelation was detected during the experiment (see “[Materials and methods](#)”)

Restoration sites and treatments

We studied 24 sites 1–5 ha in size. All sites were agricultural fields in 1939 air photos and had plantations established between 1940 and 1956 with rows of *Pinus strobus* and *P. resinosa* trees spaced 3.2 m apart. The 24 sites were randomly selected from a pool of 50 plantation areas within the study area. Before 2001 when the experiment was initiated, the 24 sites similarly had little or no hardwood regeneration taller than 20 cm, sparse understory plant cover (8% average) including tree seedlings, pine canopy cover of 60–80%, and thick (4–6 cm) Oi horizons dominated by pine needles. Fifteen of the sites received a restoration treatment of plantation removal in winter 2001 when pine trees were mechanically cut (Online Resource 2). Merchantable timber was removed and slash remained on site. Nine of the sites served as untreated controls. On restoration sites, pine density decreased by 93% and basal area by 82% after treatment, from an average pre-treatment density of 753 pines ha⁻¹ and 51 m² ha⁻¹ basal area. Controls contained 900 pines ha⁻¹ and 60 m² ha⁻¹ basal area before treatment and 751 pines ha⁻¹ and 64 m² ha⁻¹ basal area in 2015.

The 24 sites had a mean site–site distance of 2 km, and restoration sites were more spatially clustered than control sites (Fig. 1). Study site locations were constrained by where plantations were originally established and by stratified randomly selecting equal numbers (12 each) of *P. strobus* and *P. resinosa* plantations to be included in

the experiment overall and approximately equal numbers of plantations by species (eight *P. strobus* and seven *P. resinosa* plantations) to receive restoration treatments. While species of plantation did not end up as a significant factor influencing response to restoration (Abella 2010), and therefore, data were combined by pine species, this was not known a priori when a conservative approach was used to approximately balance species of plantation by treatment. Given the clustering of restoration sites resulting from these constraints, we tested for the presence of spatial autocorrelation among the 24 experimental sites using Mantel tests (Urban et al. 2002). These tests used pairwise matrices of geographic distance between the 24 sites and species composition (relative cover) derived from plot sampling described in the next section. The distance measures were Euclidean distance for the geographic matrix and Sørensen distance for the species composition matrix, with Mantel tests performed for each of the experiment’s three measurement years in PC-ORD (McCune and Mefford 1999). No significant relationship between geographic distance and species composition occurred for any year. Standardized Mantel statistics (r), similar to bivariate correlation coefficients, were low (< 0.14) and P values ranged from 0.08 to 0.57. The lack of spatial autocorrelation in the data set is consistent with variation in soil properties (Online Resource 3). Sites close to each other were frequently on different soil types, which supported different plant assemblages, resulting in little

spatial autocorrelation. Mantel tests supported using the 24 geographically separated sites as independent units in statistical analyses.

Data collection

We collected post-treatment understory vegetation data in the summers of 2002 (initial growing season after treatment), 2004 (3 years after), and 2015 (14 years after). Within a 0.05-ha (20 m × 25 m) plot in the center of each site, the areal cover of each understory vascular plant species (including tree species < 1 cm in diameter at a height of 1.4 m) rooted in the plot was categorized by the same investigator (S.R. Abella) all years as 0.1, 0.5, and at 1% intervals from 1 to 100% cover. The diameter and species were recorded for each tree ≥ 1 cm in diameter at 1.4 m.

Species nomenclature, classification as native/non-native to the U.S., and growth form (herbaceous or woody) followed Natural Resources Conservation Service (2017).

Data analysis

We modeled 24 response measures assigned to one of the four response categories of structure, richness, function, or composition corresponding to the categories of the Brudvig et al. (2017) hierarchy of predictability hypothesis (Table 1). We derived the functional and compositional variables from further tabulations or analyses of field data. We derived a wetland community index by summing the total scores of all species on a plot according to the status ranking for Ohio wetlands that classifies species as upland (1 point), facultative upland (2), facultative (3), facultative wetland (4), or

Table 1 Variability in restoration measures during 14 years of ecological restoration in the oak opening region, northwestern Ohio, USA

	Restoration		Control	
	CV (%)	Mean (range)	CV (%)	Mean (range)
Structure				
All deciduous trees (trees ha ⁻¹)	335	136 (0–2040)	183	27 (0–180)
<i>Quercus</i> (trees ha ⁻¹)	363	29 (0–660)	–	0 (0–0)
Native cover (%)	83	40 (1–107)	159	15 (1–92)
Non-native cover (%)	122	4 (0–20)	178	1 (0–7)
Woody cover (%)	106	25 (1–90)	193	12 (1–90)
Herbaceous cover (%)	83	19 (1–80)	137	3.8 (0.2–21.6)
Species richness				
Native richness (species 0.05 ha ⁻¹)	29	40 (12–64)	30	24 (13–39)
Non-native richness (species 0.05 ha ⁻¹)	64	8 (0–22)	91	3 (0–9)
Function				
Wetland index (higher = wetter)	38	100 (24–169)	37	56 (30–114)
Rare species (species 0.05 ha ⁻¹)	146	1 (0–3)	–	0 (0–0)
Floristic quality (higher = higher quality)	27	17 (8–25)	13	15 (12–20)
Butterfly plants (cover %)	173	1 (0–3)	247	0.01 (0–0.1)
Bee plants (cover %)	236	2 (0–30)	205	0.1 (0–0.6)
<i>Rubus</i> for butterfly/bee (cover %)	149	15 (0–81)	467	3 (0–64)
Composition				
Within-plot similarity through time (SS, %)	70	18 (3–51)	48	38 (4–68)
Among-plot similarity through time (SS, %)	25	24 (7–35)	42	28 (6–47)
NMS axis 1 (coordinate)	228	– 0.3 (– 1.5 to 0.9)	81	0.5 (– 1.3 to 1.0)
NMS axis 2 (coordinate)	381	0.1 (– 0.7 to 1.3)	171	– 0.2 (– 0.8 to 0.7)
<i>Rubus</i> spp. complex cover (%)	151	14 (0–80)	483	2 (0–61)
<i>Prunus serotina</i> cover (%)	232	1 (0–15)	335	4 (0–75)
<i>Dichanthelium clandestinum</i> cover (%)	326	3 (0–50)	277	0.2 (0.0–2.0)
<i>Erechtites hieraciifolius</i> cover (%)	196	2 (0–17)	403	1 (0–20)
<i>Phytolacca americana</i> cover (%)	216	2 (0–16)	374	0.3 (0.0–5.0)
<i>Andropogon gerardii</i> cover (%)	314	1 (0–20)	–	0 (0–0)

Data are separated by restoration (removal of non-native plantations) and control plots (untreated plantations), averaged across three post-treatment measurement years (1, 3, and 14 years after restoration)

CV coefficient of variation, SS Sørensen similarity, NMS non-metric multidimensional scaling

obligate wetland (5; Andreas et al. 2004). Higher values indicate communities containing species with greater affinity for wetlands. The number of conservation-priority rare species per plot was tabulated as the number of species listed as state endangered, threatened, or potentially threatened in Ohio (Ohio Department of Natural Resources, Columbus, OH, USA). We calculated a floristic quality index for each plot as the sum of species coefficients of conservatism divided by the square root of native species richness on a plot (non-native species are omitted from all calculations; Andreas et al. 2004). The coefficients of conservatism represent how restricted species are to particular habitats within landscapes and range from zero for generalist to 10 for specialist species typifying high-quality natural habitats. We summed the cover of forb and shrub species on our plots listed in the literature as utilized by the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*; Grundel et al. 2000) and by bees based on a study 8 km north of ours (Arduser 2010). *Rubus* spp. were tabulated separately as these plants are utilized by *Lycaeides* and bees. Using a matrix of all pairwise Sørensen similarities (based on relativized cover) for each plot–year combination, we calculated within-plot Sørensen similarity as the similarity a plot had to itself through time (2002:2004, 2004:2015, and 2002:2015). We also calculated average among-plot similarity within a treatment for each year. We obtained ordination axis scores, as a measure of a plot's community composition within multivariate space, using a non-metric multidimensional scaling ordination including all plot–year combinations and relative cover for species using PC-ORD's autopilot slow and thorough mode (McCune and Mefford 1999). The ordination had a final stress of 14. Axis 1 represented 46% of the variance in the plot \times species matrix, and axis 2 represented 16% of the variance. We also selected six individual taxa that were among the most abundant as example species to model for species composition.

To address our study questions, we performed two quantitative statistical analyses and one qualitative analysis to partition variance for the 24 response measures and examine the consistency of their change during restoration. We used generalized linear mixed models to partition variance attributable to the fixed effects and random plot effects, with plot as a random variable, because plots were selected from a larger pool of possible site locations. Following Selya et al. (2012), we fit initial models containing only the random plot effect (i.e., no fixed effects) and then full models including the random plot effect and fixed effects of treatment (restoration, control), year as a repeated measure (2002, 2004, and 2015 corresponding to 1, 3, and 14 years after treatment) and the treatment \times year interaction. To fit the models, we used SAS v. 9.4 with PROC GLIMMIX, which does not require that data be normally distributed, accommodating the range of our response measures including count data (e.g., number

of rare species). To examine how predictable changes in response measures were from one measurement year to the next as a function of continuous predictors, we used multiple regression (PROC REG, stepwise selection $P = 0.15$ to enter and stay, SAS v. 9.4). The following predictors were evaluated for selection by the models: pine basal area (which was a function of the restoration treatment), antecedent value of a response measure the previous measurement year (i.e., the antecedent value would be for 2002 when assessing change between 2002 and 2004), and environmental variables. The environmental variables included: distance from a plot (meters) to a Granby soil series mapping unit representing wetland soils (Stone et al. 1980); 0–15 cm mineral soil loss-on-ignition as a surrogate for organic matter, which is higher in poorly drained soils in the region (Stone et al. 1980); texture; and available water-holding capacity (Saxton and Rawls 2006). Distance to a wetland soil was included, because it was correlated with species composition in a previous investigation within the study area (Brewer and Vankat 2006). O-horizon thickness and pH (1:1 soil:water) were also screened, but excluded from models because of high correlation with other soil variables. The soil data were obtained from a previous investigation at the plots in 2004 (Abella 2010). For the qualitative assessment, we categorized the change in each response measure as decrease, no change, or increase by subtracting 2002 values from 2015 values for each plot.

Results

Plant community and response measure characteristics

There were 370 vascular plant species found on the 24 plots among years, with 153 species in 2002, 249 in 2004, and 273 in 2015. The 15 restoration plots contained 350 species among years, and the 9 control plots 150 species. Of the 370 total species, 82% were native. Of the 68 non-native species, the most frequent were *Rumex acetosella*, *Rhamnus cathartica*, *Elaeagnus umbellata*, and *Alliaria petiolata*. Native species constituted 79–95% of the total plant cover on average between treatments and years. Total species richness ranged from 12 to 79 species 0.05 ha^{-1} among plots and years. In 2015, plant cover ranged from 6–109% in restoration plots and 2–94% in control plots (one control plot had developed 75% cover of *Prunus serotina* and 94% cover overall). Dominant species in 2015 on restoration plots included several species of *Rubus*, *Dichanthelium clandestinum*, *Solidago rugosa*, *Andropogon gerardii*, *Carex swanii*, and several species of tree seedlings (e.g., *Quercus* spp., *Prunus serotina*).

Variability was high in response measures within restoration and control treatments, with coefficients of variation exceeding 80% for 75% of the measures (Table 1). Nevertheless, means of 12 of 14 structure, richness, and functional measures differed significantly ($P < 0.05$) between restoration and control treatments in one or more years and all were highest in the restoration treatment (Online Resource 4). The only two variables to not differ significantly between treatments in one or more years were the structural variables total density of deciduous trees and density of oak trees. Similar to the set of structure, richness, and functional measures, eight of ten species composition variables differed significantly between treatments in one or more years.

Variance partitioning

No clear pattern emerged in predictability among the response categories of structure, species richness, function, or composition (Fig. 2). The fixed effects of treatment and year accounted for over half of the variation in six of the 24 response measures, and these most predictable measures spanned three of the response categories. With inclusion of random plot effects along with the fixed effects, six additional response measures had over half their variability modeled. This resulted in 12 of 24 response measures with over half their variability accounted for using fixed and random

plot effects. These 12 measures were from all four response categories.

In modeling post-restoration change specifically between the first (2002) and third years (2004), 17 of 22 response measures (77%, with two measures not modeled, because their focal taxa were absent both years) had over half their variance accounted for using pine basal area, environmental variables, and antecedent value of a response measure (Fig. 3). There was no clear pattern for predictability of change between years with respect to response category, as categories contained mixtures of predictable and unpredictable measures. Changes in species composition were among the most predictable overall, even when heterogeneity of composition among sites increased (such as lowering of among-plot similarity within treatment). Predictability of change between year 3 (2004) and 14 (2015) was lower than for between years 1 and 3 for most measures, but trends among response categories remained similar. Species composition was again among the most predictable of response categories, though each category contained a mixture of predictable and unpredictable response measures.

Qualitative change

Consistency of direction of change between 2002 (first year after restoration) and 2015 (14th year after restoration)

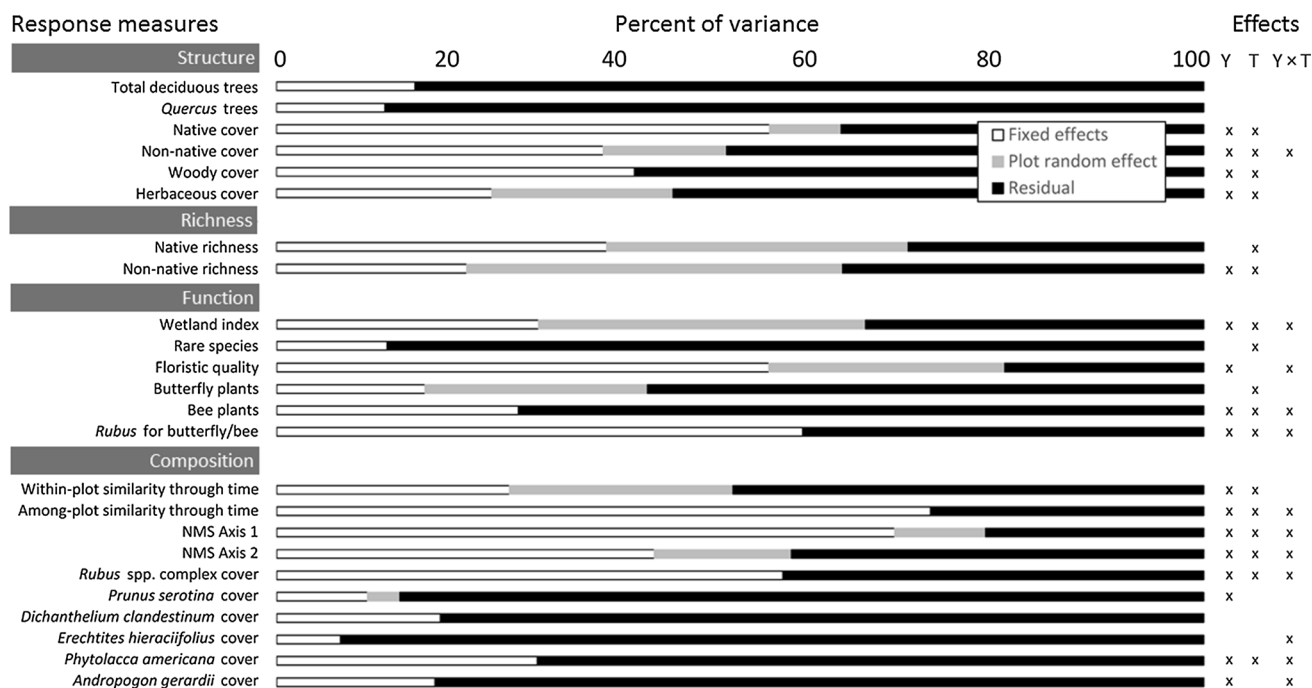
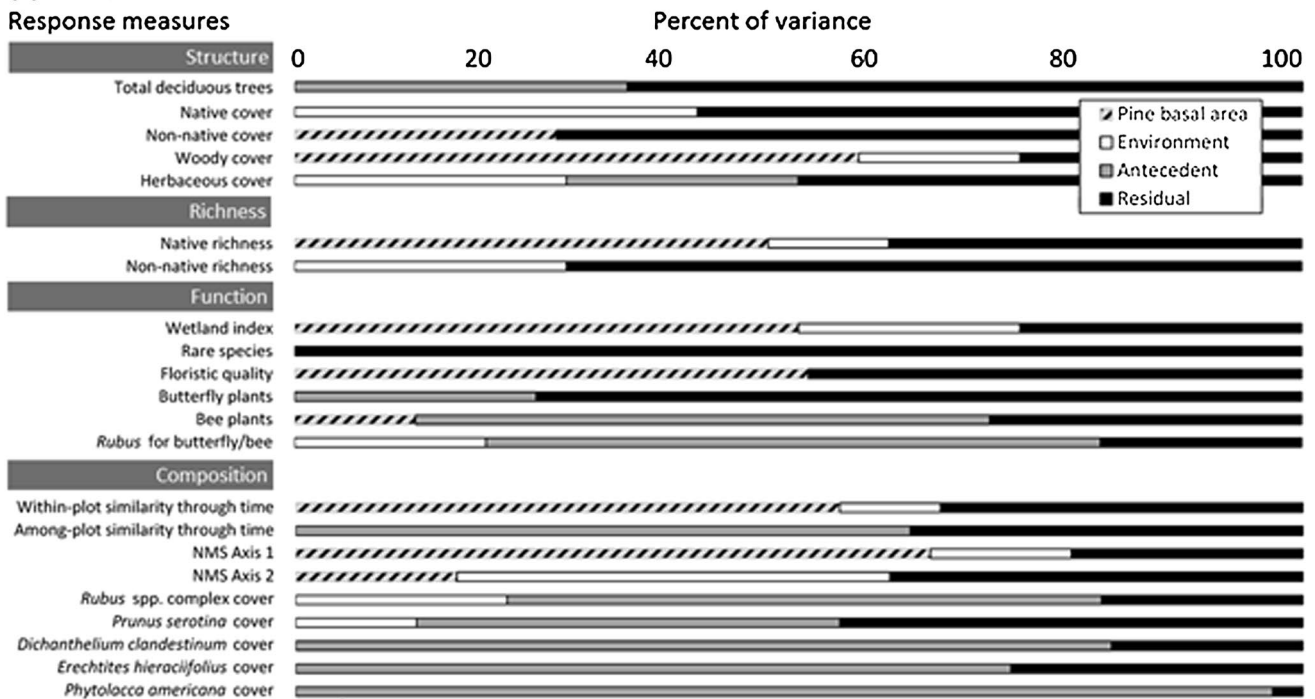


Fig. 2 Partitioning variance in response measures within four response categories into the fixed effects of restoration treatment (T) and year (Y), random effects of plot, and residual over a 14-year ecological restoration experiment in northwestern Ohio, USA. To

the right of the graph, × indicates significant effects ($P < 0.05$) of T, Y, or their interaction. Units for response measures correspond with Table 1

(a) Change between year 1 and 3



(b) Change between year 3 and 14

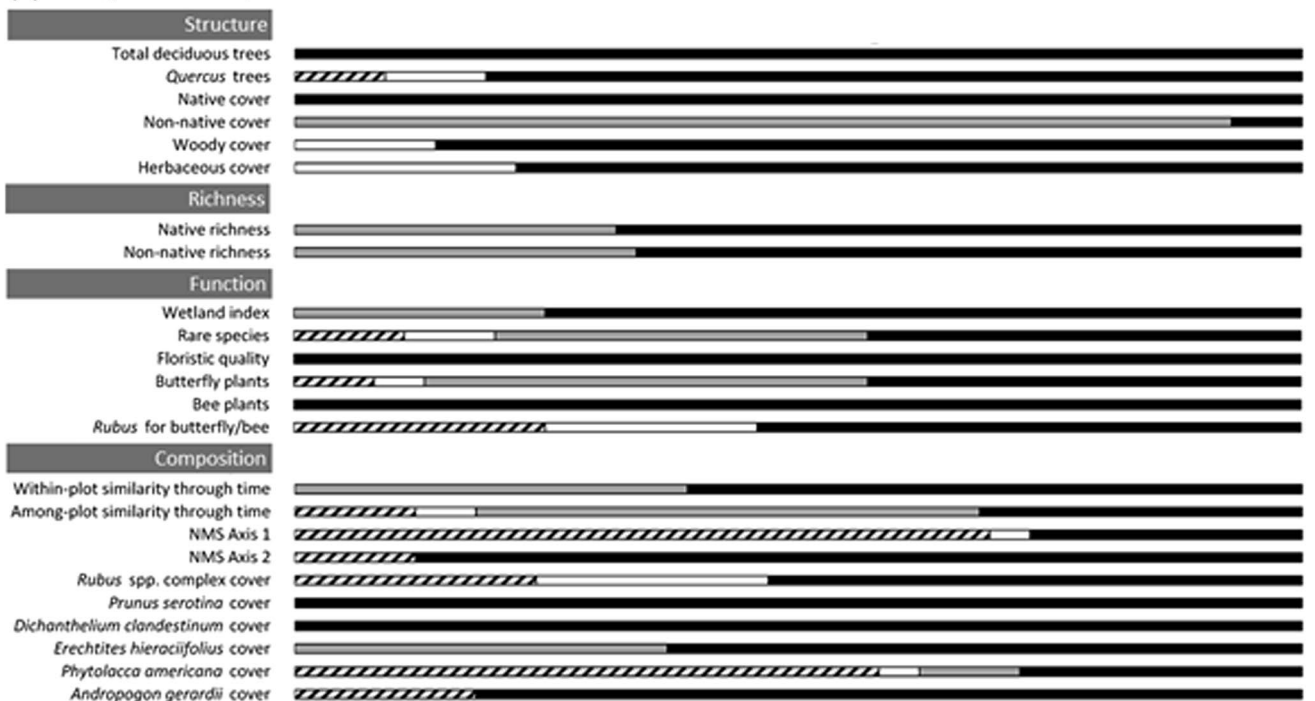


Fig. 3 Accounting for variance in response measures using pine basal area, environmental factors, and antecedent value of a response measure the prior measurement year in multiple regression modeling of change from **a** year 1–3 and **b** year 3–14 during a 14-year ecologi-

cal restoration experiment in northwestern Ohio, USA. Because they were absent from plots, *Quercus* trees and *Andropogon gerardii* are not shown in (a)

varied among response measures within response categories for both the restoration and control treatments (Fig. 4). For example, within the structure category in the restoration treatment, native plant cover increased on 93% of plots, while nearly as many plots showed decreases or no change (47%) as increases in deciduous trees (53%). The most consistently changing (> 87% of plots showing the same response) response measures after restoration spanned three of the four response categories (species richness was the exception category) and included the structural measures of native and woody plant cover, the functional measures of floristic quality, wetland index, nectar plants for bees, *Rubus* nectar plants, and the composition measures of within-plot similarity through time and cover of three of six taxa.

Discussion

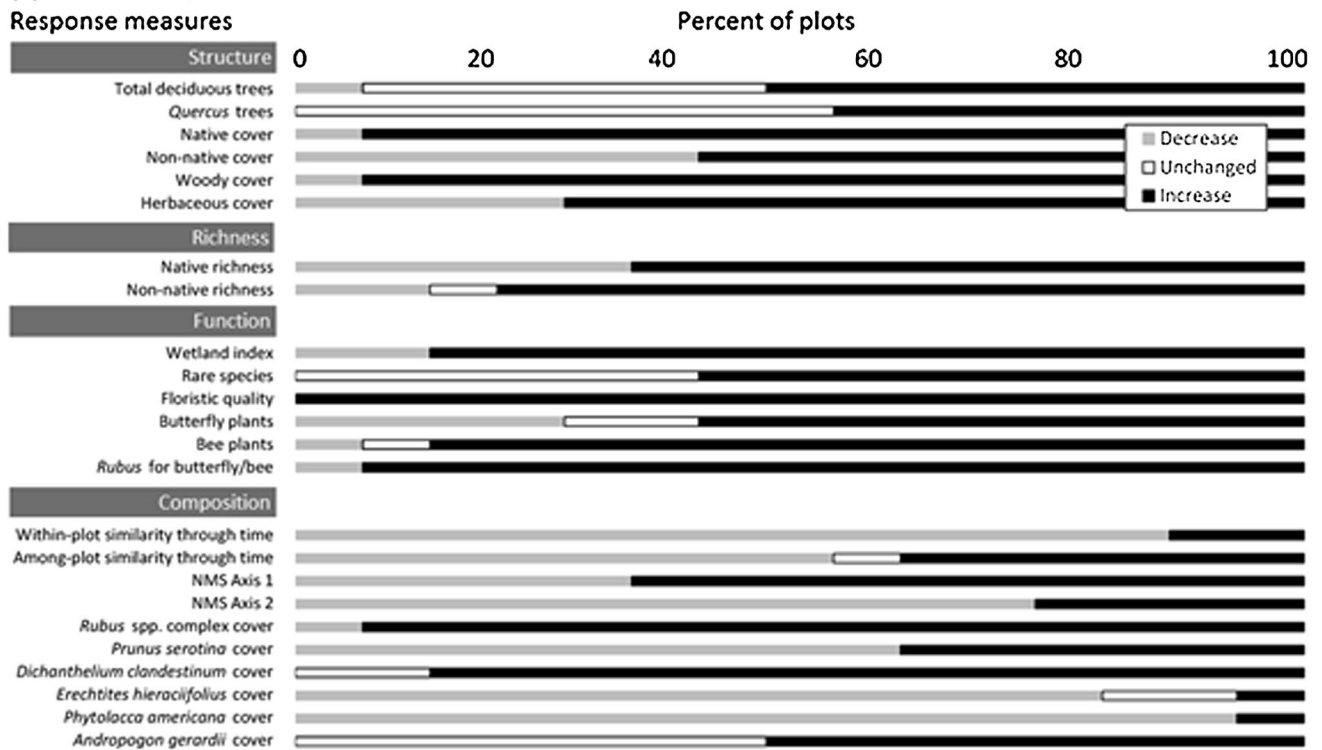
There was a high degree of predictability that a difference in the mean of a response measure would occur between restoration and control treatments during the first 14 years of restoration, but less predictability for spatial and temporal variation within treatments (among plots). However, neither the average differences (which were statistically significant for almost all response measures) nor the partitioning results for variation between and within treatments offered much support for the hierarchy of predictability hypothesis. Variance partitioning results did not display the hypothesized ordering of predictability, because response measures within categories varied in their predictability. Moreover, species composition measures, hypothesized to be the least predictable, were often among the most predictable. Results highlight a need to evaluate assumptions of the hypothesis, offer a comparison to a previous test of the hypothesis, suggest factors potentially related to variability in restoration response measures, and raise questions regarding predictive ecology in ecological restoration and succession.

A main assumption of the hierarchy of predictability hypothesis is that response variables with fewer possible permutations are easier to predict than those with more. Accordingly, variables for which species are interchangeable (e.g., total plant cover and species richness) are posited to be more predictable than those for which species identities matter, such as for species composition, theoretically arising from countless possible combinations of species and their abundances (Brudvig et al. 2017). It is unclear, though, how important the number of possible combinations of a response variable is compared to the number of possible combinations of causal factors that could affect a variable (Abella et al. 2015). For example, the establishment of a tree layer is a structural variable for which tree species are interchangeable, and thus is hypothesized to be more predictable than species composition, for which

species are not interchangeable. However, the combinations of possible causal factors related to tree layer establishment could exceed those for understory composition. One such scenario could be if tree layer establishment is contingent upon all of the community assembly factors influencing understory species composition (through mechanisms such as trees affected by understory competition, safe sites, interactions with seed dispersers or predators, and so forth mediated through understory composition), in addition to the many possible permutations of other factors (e.g., seed dispersal, predation, herbivory, and contingency effects such as weather) affecting the establishment of a tree. In other words, if tree establishment is mediated in any way through effects of understory plant composition, then all of the factors affecting understory composition, plus those affecting tree establishment in the absence of understory effects, could account for whether a tree layer develops. Ecologists are increasingly appreciating the role that species identities (and their associated species traits) can play in communities, such as through species effects on community invasibility by non-native plants (Emery and Gross 2007), plant–fungi mutualistic interactions (Gehring and Bennett 2009), and “apparent competition,” where presence of certain plant species increase animal consumer pressure on other plant species by changing the foraging behavior or abundance of consumers (Orrock and Witter 2010). It is possible that in cases where structure, species richness, and function measures are controlled by species composition, species composition itself is more predictable than these measures.

Laughlin et al. (2017), who noted they conducted the first empirical test of the hierarchy of predictability, found general support for the hypothesis during restoration of an Arizona conifer forest. Our findings were more complicated and less consistent with the hypothesis, and differences could stem from study design, ecosystem properties, and selection of restoration measures. Both experiments included random plot effects, but plots were within one site for Laughlin et al. (2017) and at 24 separate sites in our experiment. While it should not necessarily be assumed that variation among plots within one site would be less than variation among sites, it is possible that this difference in study design added heterogeneity in our experiment. Properties of the ecosystems differed between experiments, with just a single tree species for Laughlin et al. (2017) compared to 13 deciduous tree species in our experiment. There were also five times more understory species (370 compared to 74) recorded during our experiment. We included over twice as many response measures, which could only increase the chance for variation among measures within the four response categories. This raises the possibility that conformity with the hierarchy of predictability hypothesis hinges upon the particular measures selected within categories and how many measures are analyzed in each category.

(a) Restoration plots



(b) Control plots



Fig. 4 Frequency of categorical changes (decrease, no change, or increase) in response measures from 1 (2002) to 14 years (2015) after restoration in northwestern Ohio, USA. Data are the percent of plots by change category within **a** restoration and **b** control treatments

Climate, duration of the experiment, land-use history, herbivory, soil seed banks, and seed dispersal are among many factors that could have created variability in responses to restoration in our experiment. During the 2002 through 2015 study period, both annual and growing season (May through August) precipitation averaged 109% of the respective long-term averages (Online Resource 1). Within the particular vegetation measurement years, summer precipitation was 63% (2002), 114% (2004), and 155% (2015) of the long-term summer average. Annual precipitation (87, 88, and 108%) was closer to the long-term average. As a result, it is difficult to assess how variation in weather may have influenced results, because the study period as a whole was near or above average in rainfall, and the rare particular summers that were dry occurred within years of near average annual precipitation and were preceded by wet summers (Online Resource 1). This pattern may have buffered the ecosystem from more severe drought effects by limiting antecedent stress, which can mediate drought effects in Midwestern oak forests (Pedersen 1998). During an Illinois prairie restoration, Allison (2008) found that dry summers reduced total plant cover, but species responded individually including some that increased in cover during drought. Further monitoring encompassing additional years varying in precipitation would likely be needed in our experiment to ascertain how sensitive restoration outcomes are to climate.

At 14 years, our experiment is of medium-to-long duration relative to published ecological restoration projects and is representative of many of the maturing projects within the relatively young field of restoration ecology. Of 265 restoration projects published through 2012 reviewed by Wortley et al. (2013), 52% were younger than 10 years, 31% were 10–19 years, and 17% were ≥ 20 years. In future decades, in our experiment, it could be surmised that if trees survive where they have become established, they could become increasingly important filters of understory features. This could manifest through development of closed-canopy forest on plots with existing thickets of saplings and through creation of diverse sun-shade microsites on plots with developing low-density oak savanna (Leach and Givnish 1999).

All plots were under cultivation in the 1930s, though specific details about the agriculture (e.g., method of plowing, last crop type before abandonment) are not known. Such details have influenced old-field vegetation change, at least within the first 10 years, in some previous studies, but these involved a direct transition from agriculture to abandonment without another land use (e.g., Myster and Pickett 1994). Our study sites went from abandonment to being planted to conifer plantations, a land use persisting for 45–60 years until the restoration treatments at the beginning of the experiment. It seems plausible that overlaying the plantation residency for this long could have “erased” potential

legacy effects of the agricultural details among sites, but this is not known.

Herbivory, especially by irrupting white-tailed deer (*Odocoileus virginianus*) populations, is a filter of vegetation composition in many eastern North American forests (Wiegmann and Waller 2006). Extreme deer herbivory can affect not only species composition, but also structural measures such as total plant cover, height, and presence or absence of a tree regeneration layer (e.g., Asnani et al. 2006; Abrams and Johnson 2012). Deer population density is high in the study area, regularly exceeding 20 deer km⁻² (Metroparks of the Toledo Area, Toledo, OH, USA), within the range for which appreciable effects have been reported in other areas (e.g., Asnani et al. 2006). Especially if spatial effects of herbivory varied, they could have contributed to heterogeneity in responses to restoration.

Soil seed banks and seed dispersal were factors we believe were key sources of variation and complicated predicting responses to restoration. Several of the early colonizing species, such as *Erechtites hieracifolius*, *Phytolacca americana*, and *Rubus* spp., form persistent soil seed banks (Baskin and Baskin 1996; Hyatt and Casper 2000; Keyser et al. 2012). These and similar ruderal species have been detected in, while prairie and open-forest species have been absent from, the depauperate soil seed banks of other conifer plantations in the Midwest (Artigas and Boerner 1989). The deciduous tree species, such as *Acer rubrum* and *Quercus* spp., generally do not form seed banks persisting over a year (Hille Ris Lambers and Clark 2005). These observations suggest that seed banks could have affected post-restoration dynamics, but seed dispersal processes may have predominated because population changes in even the seed-bank-forming species are often dominated by dispersal processes. For example, the copious seeds of *Erechtites* are readily dispersed by wind (Darbyshire et al. 2012) and animals can disperse fruits of *Phytolacca* and *Rubus* over 100 m from parent plants (McDonnell and Stiles 1983). Predicting animal dispersal of seeds, especially in fragmented landscapes, is difficult. Seed dispersal by animals can hinge on height and structure of the vegetation and adjacent habitats (affecting animal movements), species composition of vegetation (potentially affecting animal composition and which plant species are most influenced by animals), and other factors (McDonnell and Stiles 1983; Hyatt 1998; Butaye et al. 2001). How adjoining vegetation could have influenced vegetation on plots in our experiment, such as through seed dispersal, is hard to evaluate, because there was no consistent combination of adjoining vegetation. In fact, each of the four sides of a restoration site sometimes had unique adjoining vegetation, which generally could include deciduous forest, uncut plantation, wetland, or a variety of oak savanna, woodland, and prairie ecosystems undergoing restoration activities. We did find that distance a plot was from a Granby

soil (typifying wetlands) entered some models of vegetation change, but it was not a dominant factor.

Predicting responses to restoration treatments represents a conundrum to restoration ecology. Unlike in other fields such as chemistry or engineering where a frequent goal is to minimize variation in outcomes, ecological restoration often seeks to maximize variation, or at least maintain existing variation but in alternative forms. Restoration could be viewed as specifically striving for unpredictable outcomes. As Brudvig et al. (2017) noted, a goal of prediction could simply be to help avoid restoration failures by identifying likely unfavorable outcomes for a range of possible restoration approaches under different settings. Even this task is difficult owing to numerous possible interactions within ecosystems and contingency effects. The difficulty is exemplified by how even after a century of study, successional sequences are mainly predictable only for general physiognomic features of vegetation such as cover of dominant growth forms (Meiners et al. 2015). By cutting pines and then allowing natural recovery to proceed, one viewpoint is that our experiment initiated a series of secondary successions. From that perspective, our results are similar to conclusions of many succession studies where average values for general features, such as increases in woody plants over time, are somewhat predictable, but trajectories among sites are varied and unpredictable (Prach and Walker 2011; del Moral et al. 2012). Future experiments could test whether prescribed burning, protection from herbivory, or other supplemental treatments following the overstory treatment could help guide trajectories of restoration sites.

Although many responses were unpredictable among sites, they were not necessarily undesirable and the average response was informative. The establishment of *Quercus* trees, deciduous trees overall, and rare plant species are illustrative. No *Quercus* trees became established on control plots, while eight (53%) restoration plots exhibited *Quercus* tree establishment and were developing desired savanna structure (Online Resource 2). Which plots would harbor *Quercus* tree establishment was unpredictable from any of the measured variables and essentially a 50% chance. From a restoration perspective, however, this could be considered an ideal outcome, because about half of sites could be managed as savanna or woodland and half as prairies, as all three ecosystems were historically important and are of restoration priority (Brewer and Vankat 2004). Similarly, rare plants became established on 60% of restoration plots, and while it was unpredictable as to which restoration plots would develop rare plants, no rare plants were detected on control plots during the experiment. For restoration practice, this “average” response could be viewed favorably, as there was essentially no chance rare plants would become established without restoration, while restoration created a 60% chance that plots on average would harbor a rare species. Given

that all native species measures most frequently increased or were higher on restoration plots than on controls and non-native plants declined by year 14 in restoration plots, probably the only response close to undesirable was that dense layers of non-oak trees (primarily *Acer rubrum* or *Prunus serotina*) developed on 20% of plots (e.g., Online Resource 2). This structural response was unpredictable from measured variables, which is important to evaluate further because accurately predicting where and when this tree layer develops could enable planning prescribed burns to kill these trees before they attain fire-resistant sizes (Abella et al. 2017). On the other hand, *Quercus* spp. were intermixed with the non-*Quercus* trees at two of the sites, such that they could be maintained as mixed-species forests providing unique habitat value (Grundel et al. 2010).

Results help clarify contributions that advances in predictive ecology could realistically play in ecological restoration and succession based on present knowledge. First, focusing on just predicting where outcomes are likely to be undesirable could help prioritize where to perform restoration to maximize chance of success (or identify where additional treatments are likely needed). This would be a major step forward that has generally eluded ecological restoration and efforts for promoting natural recovery through succession (Prach and Walker 2011; Brudvig et al. 2017), and may be an easier task for predictive ecology. Any outcome avoiding the undesirable range would be acceptable (Matonis et al. 2016). Second, for cases like this experiment with few negative restoration outcomes, focusing on improving prediction of the outcome averages may suffice, alleviating need for the difficult task of site-specific prediction. The average could suffice, because at worst, the response would be neutral (e.g., lack of rare plant establishment on some restoration plots in our experiment), though it could be helpful to predict neutral cases if additional resources would be available for further treatments at those sites. Third, increasing understanding of seed dispersal processes may help both prediction and resolving why results were incongruent with the hypothesis of hierarchical predictability. We propose that if seed dispersal processes are as stochastic for structural and species richness measures as they are for species composition, and if species composition mediates ecosystem processes (such as seed dispersal) affecting structure and species richness, the hypothesis of hierarchical predictability is unlikely to be supported.

Acknowledgements This study was funded by the Metroparks of the Toledo Area through a grant to Natural Resource Conservation Limited Liability Company. We thank John Jaeger for initiating the pine plantation treatments in 2001; Karen Menard and Denise Gehring for help collecting data on six plots in 2015; and two anonymous reviewers for helpful comments on the manuscript. The experiment complies with the current laws of the United States where the experiment was performed.

Author contribution statement SRA developed the study design and SRA and TAS conceived the data collection protocol; SRA and TLW collected the data, with TLW identifying plant collections; SRA analyzed the data and wrote the manuscript; and all authors edited manuscript drafts.

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