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The Effect of Restoration Methods on the Quality of the Restoration and Resistance to Invasion by Exotics

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Abstract

The methods employed in a restoration can impact the resulting plant community. This study investigated the effect of restoration method on several indices of plant community structure by comparing two restoration methods conducted over an 8-year period to a naturally colonized postagricultural field and a remnant grassland. The restoration methods included (1) distributing seed over fallow fields and (2) planting established seedlings in combination with seeding a fallow field. We found greater plant community resemblance (i.e., floristic quality, native species richness, and native diversity) to remnant grasslands with the introduction of seedlings during the first 4 years of restoration. There was also a negative correlation between the native plant diversity and the density of exotic plants in the restoration. This relationship suggests that introducing native plants in postagricultural fields may represent an effective management strategy to reduce exotic plant density.

Key words: exotic, invasive, postagriculture, restoration, succession, transplant.

Introduction

A fundamental goal of restoration was the reestablishment of plant diversity representative of native remnants (Kline 1997*a*). Although progress has been made in this direction, many restorations do not attain this goal, as demonstrated by multiple indices, including richness, which plateaus or declines with restoration age, and both small scale (α) diversity and structure that are reduced in restorations relative to remnants (Sluis 2002; Lunt 2003; Ammann & Nyberg 2005; Martin et al. 2005; Polley et al. 2005; Cousins & Aggemyr 2008; Smits et al. 2008). Factors limiting the successful restoration of native diversity are not well understood and our knowledge of these factors is limited in part because there are few quantitative assessments of restorations performed in a replicated framework. Here, we assess the effectiveness of two different restoration methods in reproducing community characteristics of native remnants.

The observed differences in plant community structure between restorations and remnants may be attributed to factors influencing recruitment from the seed bank or to dispersal limitations (Lenz & Facelli 2005; Polley et al. 2005). Many restorations have been initiated on former agricultural land (Kline 1997*b*), where long-term tillage and herbicide use or intense grazing have reduced plant propagules native to the original ecosystem in the soil seed bank (Lunt 2003). Even in remnant grasslands, some seeds do not persist in the soil seed bank (Rabinowitz & Rapp 1980; Tekle & Bekele 2000), likely contributing to the limited success of restorations. Adding to the problem of natural recolonization is the fact that in many grasslands, there are few remaining native stands and many native species have limited dispersal (Tilman 1997; Ricketts et al. 1999; Seabloom et al. 2003; Martin & Wilsey 2006). Thus, restoration generally requires not only seed addition but also an established, natural seed source to allow for multiple reintroductions (Kindscher & Tieszen 1998; Muller et al. 1998; Ricketts et al. 1999; Tekle & Bekele 2000; Ewing 2002).

Independent of seed limitation, restoration success may be affected by how the restorations are established and maintained. Community establishment can be influenced by how seeds are sown, for example, drilled, hand broadcast, or hand-planted seedlings (Bakker et al. 2003). In addition, altering the proportion of grasses to forbs used in the seed mix, fire regime, and presence of grazers postplanting all can influence the trajectory of developing communities (Howe 1995; Howe & Brown 1999; Copeland et al. 2002; Bakker et al. 2003; Towne et al. 2005). Furthermore, community trajectories can shift because a subset of the species is more successful reproducing vegetatively than by seed (Morgan 1999; Benson & Hartnett 2006).

Restoration of native diversity can be particularly sensitive to variation in seedling establishment. For example, the J.T. Curtis Prairie in Wisconsin (United Sates), the oldest and a particularly successful prairie restoration, was initially revegetated with prairie plants using prairie sod from remnants (Cottam & Wilson 1966). Although there are few studies that have evaluated whether hand-planted seedlings improve the quality of restorations, as indexed

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by species richness or diversity, transplanted seedlings survive at a higher rate than seedlings germinating from seed in the field (O'Dwyer & Attiwill 2000; Richter & Stutz 2002; Page & Bork 2005; Buisson et al. 2006). The investment of time and resources in planting seedlings fosters survivorship through a critical life stage (Clark & Wilson 2003). In addition, tending to the seedlings in controlled conditions, as opposed to seeding into a field, prevents seed predation of costly or rare seed (Howe & Brown 1999; Zorn-Arnold et al. 2006).

Because most prairie restorations are established in former agricultural fields, many of the aggressive and often exotic weed species persist during restoration. Contrary to the notion that exotic species are generally more competitive than native plants, the introduction and management (i.e., proper fire regime) of natives can provide them with a competitive advantage over exotics (Blumenthal et al. 2005; Suding & Gross 2006). The establishment advantage of natives in restorations may occur even with no competitive advantage if adding viable native seed swamps the seed bank in favor of native species.

In this study, we compared multiple indices of plant community structure between a postagricultural field, a remnant tall grass prairie, and multiple parcels of land restored to prairie using two different restoration approaches. We evaluated whether there was a significant benefit to hand-planting seedlings in seeded restorations with respect to native richness and α and β diversity. We also tested whether successful restoration of native plants influences the density of postagricultural exotic species during restoration.

Methods

Study Sites and Restoration Approaches

The Kankakee marsh region in northwestern Indiana (United States) was once covered by a large, shallow lake and was part of the wetland complex of the Kankakee River. In the early 1900s, this area was drained and subsequently cultivated for approximately 50 years. The Kankakee marsh region has a complex land-use history, and the four sites in this study differed in agricultural history and current land use: remnant prairie (never tilled, maintained as prairie), fallow postagricultural land, and parcels of land restored using two different restoration approaches, both tilled in the past (Table 1). The remnant native prairies consisted of a small mesic prairie surrounded by postagricultural land undergoing restoration (lat 41°05′N, long 87°25′W) and a wet to mesic sand prairie located within the Iroquois County Conservation Area in Illinois, United States (lat 40°95′N, long 87°33′W). The fallow field is adjacent to the mesic prairie. Before 1950, agriculture ceased and the field has been naturally colonized.

The seeded restoration is located in Newton County, Indiana, United States (lat 41°04′N, long 87°24′W). The restoration began in 1998 and in that year, the first parcel was restored by seeding with a seed drill. The following 2 years (1999 and 2000), seed was broadcast with a fertilizer spreader. For all subsequent years (2001–2004), two types of parcels were restored. Either the parcel had been fallow because the purchase of the land or the parcel was in corn–soybean crop rotation. Fallow land received at least one spring application of Roundup or a Roundup and 2,4-D mixture (Monsanto Company, St. Louis, MO, U.S.A.; Agriliance, LLC., St. Paul, MN, U.S.A.) taking care to avoid established prairie plants. The fallow land was then burned in the fall to remove standing vegetation. If the land was leased for agriculture and planted with Roundup-ready soybeans (Monsanto Company), the soybeans were harvested. If the land was planted with corn, the area was harvested and tilled. Each parcel represented a single year of restoration effort (Table 1). A different portion of the property was restored by seeding each year from 1998 to 2004 (Table 1).

Seed used in the restoration plantings was collected from an on-site nursery or off-site prairie within a 15-mile radius of the restoration. In late fall, site-specific seed mixes were created and seed was spread using a broadcast spreader with or without a cultipactor, depending on most recent land use. In the first growing season of a newly planted restoration, the area was mowed if weedy annuals dominated. In subsequent years, invasive plant infestations were treated with the appropriate herbicide. Within the first 5 years, most new restoration plantings were burned at least twice.

The second restoration treatment (seedling + seed restoration) was established as part of a soil amendment experiment (only the unamended treatment is included in this study). Within this study, 2 × 2–m subplots were planted with prairie seedlings and a seed mix. These subplots were spaced within a 14 × 42–m array (henceforth

Table 1. Summary of sampling sites, representative years, and the number of plots sampled.

Site Name	*Year*	*Number of Plots Sampled*
Postagricultural field	1950	Four
Remnant	Pre-1900	Two per site
Restorations		
Seed	1998, 1999, 2000, 2001, 2002, 2003, 2004	Four per year
Seedling + seed	2001, 2002, 2003, 2004	One per year

called "plots"). Replicate plots were established each year from 2001 to 2004, but the size was reduced to 14 × 24–m with a total of 18 subplots from 2002 to 2004. The seed used in this experiment was from the same pool of seed harvested for restorations each year. Seeds were cold moist stratified for 10 days in moist Scott's MetroMix (The Scott's Company, Marysville, OH, U.S.A.) and germinated. Approximately 3 weeks before, the plants were established in the field and they were planted in Root-trainers (Steuwe and Sons, Corvallis, OR, U.S.A.) with sterilized soil collected from the planting site. In all years, a hexagonal array was used to plant 21 seedlings of 11 species in a random order. With the exception of the 2004 plot, which was treated with herbicide before planting, the plots were not treated with herbicide before or after planting. The 2004 plots were burned in fall 2004 and all plots were burned in March 2005.

Vegetation Sampling

Because the seedling + seed restoration had permanently established subplots, we imposed the same design in the seed restorations. Sampling the seed restorations began by identifying the largest continuous parcel of land (each restoration year sampled) and dividing it into four quadrants. Within each quadrant, one 14 × 24–m plot was randomly selected and marked. Within each plot, six 2 × 2–m subplots were randomly chosen and sampled. This sampling design allowed us to assess plant diversity and composition at the 2- and the 14-m scale. A total of four plots (24 subplots) were sampled each year for the seed restoration and in the postagricultural field. Because of the small size of both of the prairie remnants, two plots (12 subplots) were sampled in each portion of the remnant using the same procedure as described above (Table 1).

Vegetation composition was assessed within the subplots according to the point intercept method using a grid consisting of 45 intersections (Barbour et al. 1999). At each intersection, a 1-m-long bicycle spoke was extended into the vegetation. Each plant that touched the spoke was identified and the number of times that an individual plant touched the spoke was also recorded. In the seedling + seed restoration, the boundaries of the subplots had been previously outlined and all subplots were sampled.

Plant species occurrence and abundance data from each subplot obtained from the point intercept method were used to calculate species density, species richness, evenness, Shannon's index of diversity (Hayek & Buzas 1997), coefficient of conservatism (Swink & Wilhelm 1994), and floristic quality index (FQI) (Swink & Wilhelm 1994). Species density is defined as the total number of touches of a species in each subplot. Coefficient of conservatism or C values represent an index (scaled from 0 to 10) assigned to native species based on their likelihood to be found in undisturbed, remnant lands (Swink & Wilhelm 1994). The mean C value of an area can be used to roughly describe its successional stage; many plants in remnant grasslands have high C values and plants in a newly fallow field generally have low C values. FQI is an index created to evaluate site quality based on mean C value and the number of natives present.

Data Analysis

We tested for differences in plant community structure at a small scale (subplot) as well as a larger scale (plot) (Table 1). We used the MIXED procedure in SAS (SAS Institute, Cary, NC, U.S.A.) to analyze community structure in subplots, with year and plot nested within year and the interaction of year and method identified as random effects. Plot-scale measures were calculated by pooling subplots within plots (Table 1) and analyzed using year and the interaction between year and method as random effects. Plant density, species richness, density of natives, and FQI were square root transformed to minimize heterogeneity of variance. The postagricultural field and remnant prairie were excluded from tests of restoration methods.

We also evaluated the relationship between native diversity and exotic density using correlation. Although native composition was manipulated through restoration method, the exotic plant density and composition were not. We tested the hypothesis that successful establishment of native prairie plant species suppresses exotic weeds at the local scale by including native diversity as a covariate along with year, and restoration method on subplot level measures of exotic diversity, exotic richness, and density of exotics. The analysis used proc MIXED as above. To be conservative, we identified the interactions of native diversity with year and plot within year as random effects, thereby testing the covariate over the variation in the relationship between years.

Results

After 50+ years postagriculture, the fallow field more closely resembled the restorations than the remnants as measured by FQI, species richness, evenness, and species diversity. The mean C value was not different between the remnant and the fallow field (Fig. 1a), likely because a few later successional species from the remnants were able to colonize the postagricultural field.

The seedling + seed restoration had more later successional species establish than the seed-only restorations. The mean C value was similar between restoration methods at both scales (Fig. 1a). The FQI was higher in the seedling + seed restoration than the seed restoration (Fig. 1b; subplot: $F_{[1,3]} = 15.64$, $p = 0.029$; plot: $F_{[1,3]} = 4.33$, $p = 0.13$).

The seedling + seed restoration more successfully attained the richness, diversity, and density found in a remnant prairie than the seed-only restoration. Total richness for the seed-only restoration was variable by

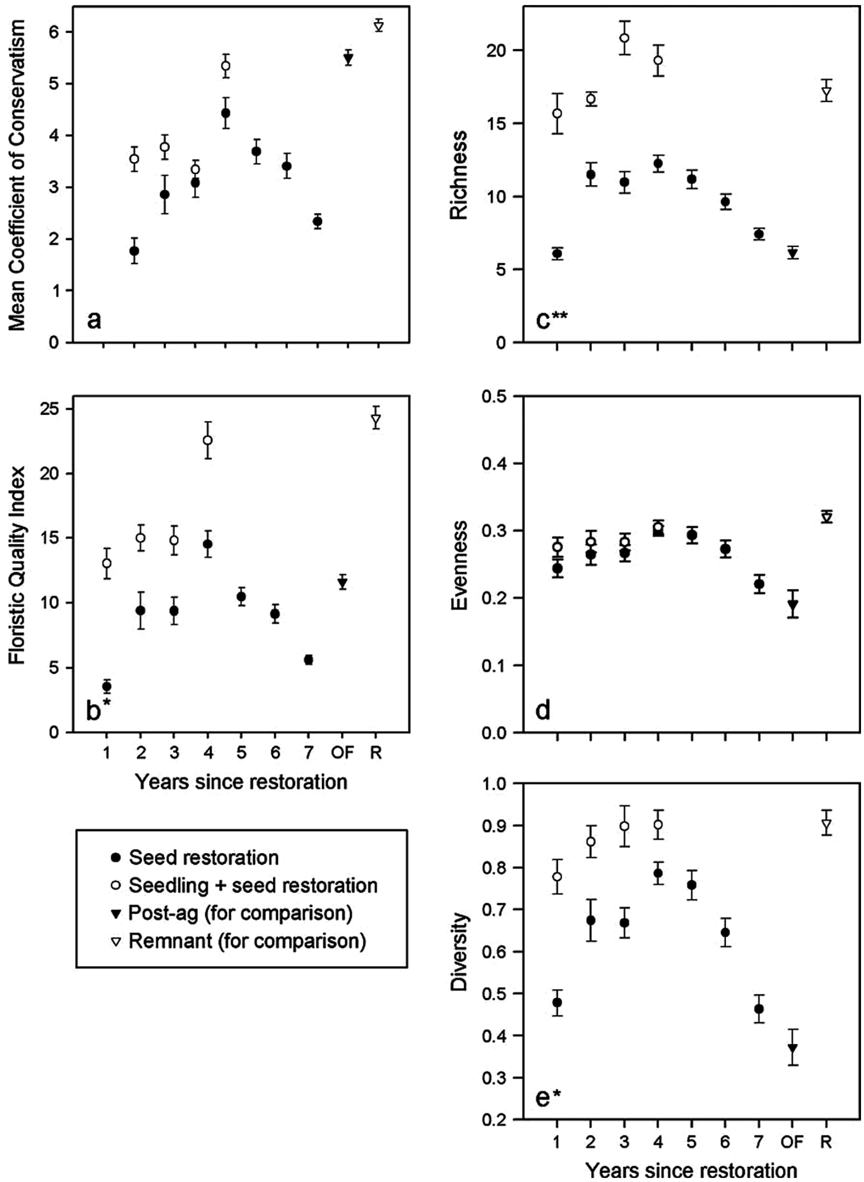

Figure 1. Plotted means ± SE by subplot for (a) mean coefficient of conservatism, (b) FQI, (c) richness, (d) evenness, (e) and diversity. Years since restoration refers to how many years it has been since the restored areas were planted. The postagriculture and remnant points are shown for reference as initial and target endpoints but were not included in the statistical analysis. A "*" or "**" by the panel letter refers to whether the variable was significantly different at the subplot scale ("*") or both subplot and plot scales ("**") at the $p \leq 0.05$ level.

year and was lower than the seedling + seed restoration at both the plot and the subplot scales (Fig. 1c; subplot: $F_{[1,3]} = 38.75$, $p = 0.008$; plot: $F_{[1,3]} = 11.38$, $p = 0.043$). Native richness was greater in the seedling + seed restoration than in the seed restoration (subplot: $F_{[1,3]} = 18.19$, $p = 0.024$; plot: $F_{[1,3]} = 16.50$, $p = 0.027$). Evenness did not change over time, nor was this index influenced by restoration method (Fig. 1d). Total diversity was lower in the seed restorations than in the seedling + seed restoration at the subplot scale (Fig. 1e; subplot: $F_{[1,3]} = 20.27$, $p = 0.021$; plot: $F_{[1,3]} = 3.67$, $p = 0.15$). Native plant diversity was significantly higher in the seedling + seed restoration than the seed restoration (subplot: $F_{[1,3]} = 44.79$, $p = 0.0068$; plot: $F_{[1,3]} = 16.50$, $p = 0.027$). Density of native plants in the seedling + seed restoration was higher than the seed restorations and most similar to the remnants (subplot: $F_{[1,3]} = 12.86$, $p = 0.037$; plot: $F_{[1,3]} = 0.05$, $p = 0.838$).

In both restorations, the diversity of the native community affected the cover of exotics. Density of exotics was negatively correlated with native diversity within restoration subplots ($r = -0.429$, $n = 253$, $p < 0.001$; Fig. 2). Including the native diversity as a covariate within analysis of exotic density suggested that increased establishment of

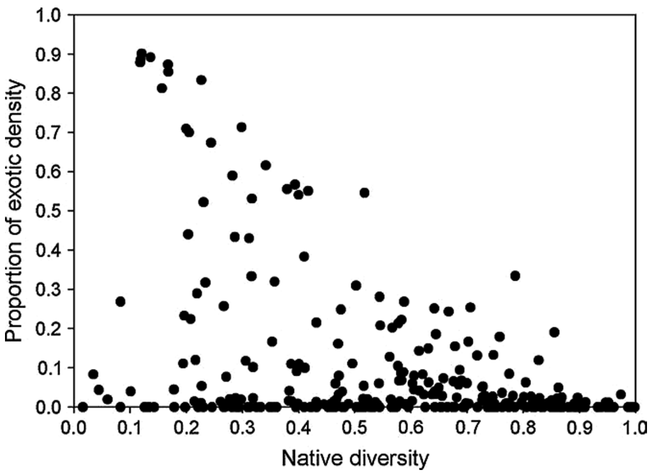

Figure 2. The relationship between native diversity on the density of exotics.

native diversity significantly decreased the density of exotics found in the restorations ($F_{[1,6]} = 16.28$, $p = 0.007$). The negative effect of native establishment on exotic plant density accounted for the differences in exotic plant density observed between the two restoration methods.

Discussion

Colonization of Postagricultural Land Takes Time

We found that when source populations were available to postagricultural land, recolonization by some species occurred. However, after 50 years, postagricultural land did not resemble a prairie. The most abundant species that colonized were Little bluestem (*Schizachyrium scoparius*) and Marsh blazing star (*Liatris spicata*) (E. Middleton, unpublished data). The colonization of these two species would be expected given that they have seed structures adapted to wind dispersal—the pappus for *L. spicata* and a densely ciliate fruiting structure for *S. scoparius* (Gleason & Cronquist 1991). Other species that were present in nearby remnant prairie but absent in the post-agricultural field were likely missing due to seed limitation (Rabinowitz & Rapp 1980; Seabloom et al. 2003; Benson & Hartnett 2006; Leps et al. 2007).

Method Matters

The seed-only restorations were more similar to prairie remnants than natural colonization at both the subplot and the plot scales. However, the restorations still remained less diverse and species rich than the remnants. We found that incorporating seedlings in addition to seeding improved the overall native richness, diversity, and quality of a restoration, suggesting that restoration by seeds alone is limited by the seedling life history stage (Otsus & Zobel 2002; Clark & Wilson 2003). The seedling + seed restoration was higher in quality than the seed-only restorations over the first 4 years of establishment. Although the seedling + seed method has only been evaluated over a few years, natives have very high survivorship once the seedlings have survived into their second growing season (P. Schultz 2008, Indiana University, personal communication). The survival of perennials into subsequent growing seasons suggests that native diversity will plateau and not decline over time.

In three of the seedling + seed restoration years, total diversity was nearly equivalent to the remnants' levels. This finding is in contrast to Polley et al. (2005) where remnant α and β diversity were higher for the remnants where restorations were established by prairie remnant hay. The seedling + seed restoration was most similar to remnant prairie when they are compared at the subplot (α) scale. In ecosystems where diversity is not due to heterogeneous topography, it may be particularly important to reestablish small-scale patterns of diversity in remnants.

Planting seedlings may also reduce the loss of native richness over time. Native richness increased for the first 4 years as the prairie perennials established, as expected from observations of succession (Nicholson & Monk 1974; Bazzaz 1975). However, native richness declined in the older seed restorations. This pattern is mirrored in Sluis (2002), who found a decrease in species richness as restoration age increased. Sluis (2002) attributed the decline in species richness over age, in part, to the gradual loss of annuals. We also observed a decrease in native and total diversity, native and total richness with age, but there was no corresponding increase in mean C value or FQI for the oldest restorations as would be expected from a loss of annuals. Moreover, as most species planted in the seedling + seed restoration are long-lived perennials, we do not expect a decline in diversity over time. Alternatively, we suggest that the decline in quality in older restorations resulted from restoration methods improving over the first few years. This reasoning may also explain the results from Sluis (2002) as each age of restoration represents a different tract of land. Additional restoration chronosequences are needed to evaluate these hypotheses.

Investing effort in germinating, establishing, and transplanting ecosystem-specific perennial seedlings can result in an increase in target species establishment. This technique may also be useful for nitrogen fixers that need to be inoculated with rhizobia or plant species that are obligately mycorrhizal because it can be ensured that the seedlings have been planted with their appropriate symbionts (Bever et al. 2003). Restoration with seedlings has been successfully applied to other systems such as coastal communities, tropical and Mediterranean forests, deserts, and wetlands (Morgan 1999; Fraser & Kindscher 2001; Li et al. 2004; Pausas et al. 2004; Griscom et al. 2005; Paling et al. 2007).

Revegetation With Natives as an Effective Exotic Management Strategy

The successful establishment of native diversity limited the density of exotic weeds. The negative correlation of native diversity and exotic density was not a result of manipulation by restoration practice nor because plants were space limited. The number of species found in any restoration year was uncorrelated with the number of touches during point intercept sampling. It is important to note that although native diversity was manipulated during restoration, exotic density was not. In fact, the inclusion of native diversity as a covariate removed the significance of restoration method, as would be expected if the improved native establishment with planting of seedlings mediated the decreased density of exotic species. Therefore, the decreased density of exotic species was not a by-product of measurement but of competition from natives. Our findings agree with Blumenthal et al. (2003, 2005), which indicates that the establishment of natives may dampen invasion by outcompeting most exotic species.

Quantitative evaluation of restorations provides information on methods and management practices to restore communities. Our work demonstrates that the addition of seedlings into a restoration can be an effective strategy to improve success in restoring the plant community to a remnant-like state. In addition, we found that restorations with seedlings and higher diversity effectively suppressed exotic plant species and exotics were inversely correlated with native species diversity. Thus, restoration can be viewed as a tactic to combat the invasion of exotic species.

Implications for Practice

- The resemblance of restorations to remnant land may improve with transplanted seedlings in addition to seeding methods.
- Adding seedling transplants resulted in higher native diversity, native richness, FQI, and mean coefficient of conservatism values.
- Across different restoration methods, native diversity has a suppressive effect on exotic plant density. This suggests that the added effort of planting seedlings may pay off as reduced effort in weed management in subsequent years.

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