

RESEARCH ARTICLE

Ecosystem Changes Following Restoration of a Buckthorn-Invaded Woodland

Daniel J. Larkin,^{1,2} James F. Steffen,¹ Rachel M. Gentile,^{1,†} and Chad R. Zirbel^{1,‡}

Abstract

Shifts in plant-community composition following habitat degradation and species invasions can alter ecosystem structure and performance of ecosystem services. In temperate North American woodlands, invasion by aggressive Eurasian shrubs has produced dense thickets with depauperate understory vegetation and increased rates of litter decomposition and nutrient cycling, attributes that could impair storage of carbon as soil organic matter (SOM). It is important to know if such impairment has occurred and, if so, the extent to which restoration can return this service. We used an oak-woodland restoration chronosequence in northeastern Illinois to contrast structural and functional attributes of unrestored areas dominated by *Rhamnus cathartica* (common buckthorn) with areas that had undergone buckthorn removal and ongoing, active management for less than 1 to 14 years. With increasing age, restored

areas had higher understory plant diversity and cover ($p < 0.0001$ and 0.005 , respectively) and higher litter mass ($p = 0.018$). These structural differences were associated with some evidence of reduced soil erosion ($p = 0.027–0.135$) but greater soil CO₂ efflux ($p = 0.020–0.033$). Total particulate organic matter (POM) in the soil increased with restoration age, which was driven by increases in the slow-turnover, mineral-associated SOM fraction. However, variance was high and relationships were only weakly significant ($p = 0.082$ and 0.083 for total POM and mineral-associated SOM, respectively). Our results suggest that, in addition to better documented biodiversity benefits, beneficial changes to ecosystem properties and processes may also occur with active, long-term restoration of degraded woodlands.

Key words: carbon sequestration, chronosequence, erosion, plant diversity, *Rhamnus cathartica*, soil organic matter.

Introduction

Ecosystem services increasingly motivate restoration (Ruiz-Jaen & Aide 2005a; Aronson et al. 2010), but the focus primarily remains on reestablishing structure in terms of native vegetation (Ruiz-Jaen & Aide 2005b) and potential enhancements to ecosystem functions are often not quantified (Aronson et al. 2010). This is problematic as diverse goals of restoration are not always mutually compatible (Hansson et al. 2005; Rieman et al. 2010). For example, hydrologic and water-quality services in wetlands can conflict with biodiversity support (Zedler 2003).

One ecosystem service that can be influenced by restoration-driven vegetation change is storage of carbon (C) in soil organic matter (SOM) (Baer et al. 2002). Functional traits that differ among plant species affect C capture and release (De Deyn et al. 2008). As restoration changes plant-community

composition, it may alter C-storage potential. For example, transitioning from invasive plant dominance to diverse, native communities is a common restoration goal. Invasive species can alter ecosystem processes in ways that either increase C storage (e.g. high productivity, recalcitrant litter) or decrease C storage (e.g. loss of biodiversity-associated functioning, increased mineralization, labile litter) (Ehrenfeld 2003). Thus, restoration may change C cycling, but the direction will be context-dependent. While there is great interest in restoration as a means to sequester C (Swingland 2002; Curran et al. 2012), there are concerns regarding the adequacy of the science, the feasibility of meaningful fossil-fuel offsets, and the quality of restorations likely to result from C markets (Galatowitsch 2009; Fissore et al. 2010).

Temperate U.S. woodlands have been degraded by invasions of Eurasian shrubs, such as *Berberis thunbergii* (Japanese barberry), *Ligustrum vulgare* (common privet), *Lonicera* spp. (honeysuckles), and *Rhamnus cathartica* (common buckthorn). These species produce dense thickets that displace native species, reduce light, and alter ecosystem processes (Ehrenfeld 2003; Yates et al. 2004; Knight et al. 2007)—changes likely to influence SOM storage. Such thickets might appear to provide opportunities for storage of C as woody biomass. However, C capture benefits of fast-growing shrubs may come at a cost to other ecosystem C pools.

¹Plant Science and Conservation, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, U.S.A.

²Address correspondence to D. J. Larkin, email dlarkin@chicagobotanic.org

[†] Present address: Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, U.S.A.

[‡] Present address: Department of Plant Biology, Michigan State University, East Lansing, MI 48824, U.S.A.

In the Chicago U.S. region, forest condition has been impacted by the invasion of common buckthorn, which has caused large areas of woodland to lose their characteristic open-canopied structure. Correlates of buckthorn dominance include low understory plant diversity, rapid litter decomposition, altered soil chemistry, and increased earthworm abundance (Knight et al. 2007; Madritch & Lindroth 2009). In our study site, Heneghan et al. (2004, 2006, 2007) found that buckthorn invasion was associated with elevated soil nitrogen and pH, altered nitrogen cycling, and reduced litter mass, compounded by a positive feedback between buckthorn and earthworms.

We used the common practice of buckthorn removal followed by restoration of native vegetation to investigate ecosystem changes that could influence C storage. We expected restoration to increase understory plant diversity and cover, leading to greater SOM stock. We also quantified processes—soil erosion and CO₂ efflux—that could result in ecosystem C loss. We predicted the following correlates of restoration age: (1) a more characteristic woodland canopy, with higher oak importance and openness due to buckthorn removal and increased space and light; (2) higher understory diversity and cover and distinct composition from invasive-species removal, seeding, and burning; (3) litter layer recovery because of increased understory vegetation and reduced amounts of labile buckthorn litter; (4) decreased soil erosion through stabilizing vegetation and litter; (5) lower soil CO₂ efflux due to decreased labile buckthorn litter and buckthorn-associated earthworms that promote mineralization; and (6) higher soil C storage through movement of plant-derived C to SOM pools.

Methods

Study Site and Design

We conducted this study in McDonald Woods, located in northeastern Illinois (lat 42°9'N, long 87°46'W), a 40-ha site in the central forest/grassland transition ecoregion (Ricketts et al. 1999). The site was managed as a natural area, with mesic and dry-mesic woodland, flatwoods, wetland, and savanna habitats. Past disturbances included logging, grazing, fire suppression, erosion, and dense populations of white-tailed deer and invasion by exotic earthworms and plants.

Restoration of McDonald Woods began in the late 1980s. The goals were to eradicate buckthorn and other invasive plants and reestablish an open-canopied woodland with high biotic diversity and ecosystem functioning. For understory vegetation, targets included high native-species diversity and high cover of graminoids. Management actions included revegetating eroded gullies, removing buckthorn and other invasive species, and prescribed burning in patches, with areas typically burned (as surface fires) every 4–5 years. About 150 native plant species were added as seed, including 30 sedge, 16 woodland grass, and 25 Asteraceae species. Restoration was conducted in discrete patches over time, yielding a chronosequence of restored areas less than 1 to 3 ha that ranged



Figure 1. Unrestored and restored areas in McDonald Woods. (a) Common buckthorn was the dominant vegetation in unrestored areas; note the lack of understory vegetation and abundant bare ground. (b) Restored areas had greater canopy openness and understories with diverse herbaceous vegetation.

from less than 1 year to more than 20 years old. There were also buckthorn-dominated, unrestored stands (Fig. 1). Timing and location of restoration was based on resource availability and proximity to already restored areas.

We used a chronosequence design (space-for-time substitution) to compare areas of degraded and restored dry-mesic oak woodland along a moraine slope. There were no nearby oak-woodland stands that had not been invaded and/or restored that could serve as suitable reference controls. In summer 2009, we established 50-m × 50-m (0.25-ha) chronosequence plots in an unrestored control and in patches restored in 2003, 2001, and 1996 ($n = 1$ for each). In summer 2010, we established new 0.25-ha chronosequence plots, including a newly restored patch (winter 2010) ($n = 1$) and previously unsampled locations within the unrestored ($n = 2$), 2003-restored ($n = 2$), and 1996-restored areas ($n = 2$) (Fig. 2). Locations restored in other years were excluded because they were substantially smaller or differed in topography or other attributes. Unrestored controls appeared similar to the starting condition of restored areas but we lack pre-restoration data to account for pre-existing differences. The unrestored and newly restored areas had not been burned, but all other restored areas were burned 1–3 years prior to this study.

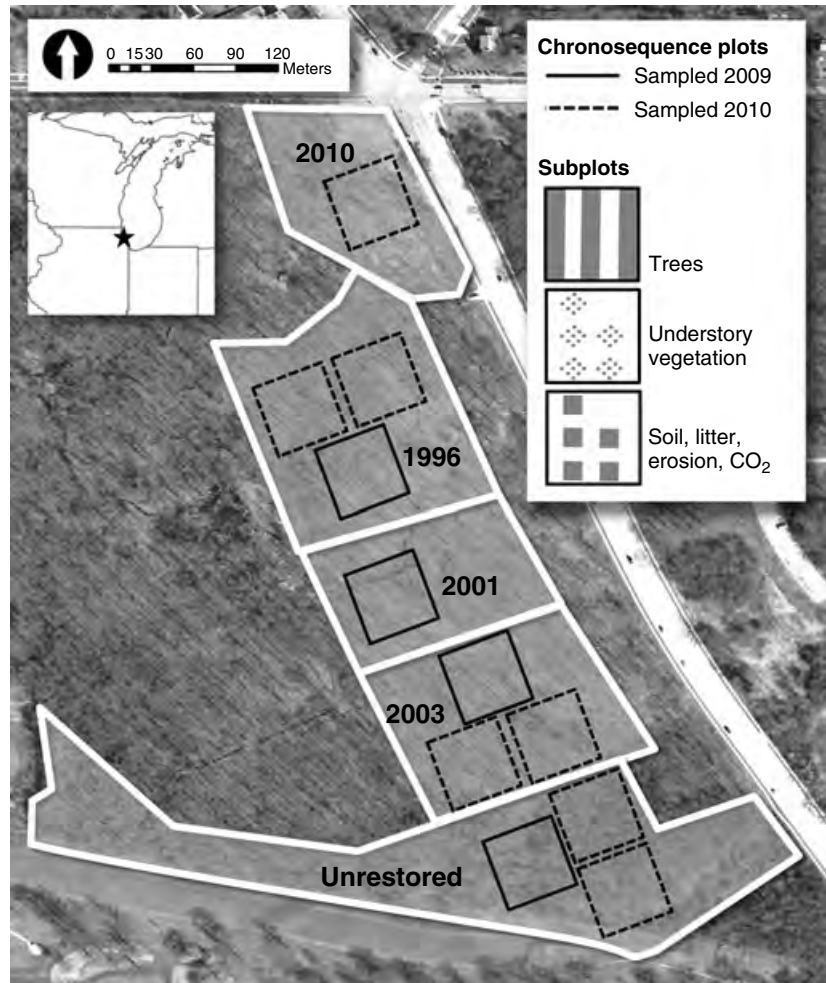


Figure 2. Map of the study area in McDonald Woods showing the locations of restoration treatments and the arrangements of chronosequence plots and sampling subplots.

We measured tree composition, understory plant diversity and cover, litter mass, soil CO₂ efflux, soil erosion, and SOM in subplots within each chronosequence plot (Fig. 2).

Plant Community Structure

We measured tree composition in 2009. Within each chronosequence plot, we recorded species and diameter at breast height (DBH) of all trees (DBH \geq 3 cm) within three, parallel 50-m \times 10-m belt transects (Fig. 2). For multi-stemmed individuals, DBH of the largest stem was recorded. Species' importance percentages were calculated as the means of relative density, frequency, and basal area (BA).

Understory vegetation and litter were sampled in late July of 2009 and 2010. Within each chronosequence plot, quadrats were systematically positioned in and around each soil subplot (Fig. 2). All herbaceous plants and short woody plants (<1 m) were identified to species or the lowest feasible taxon and abundance was recorded using Braun–Blanquet cover classes (cover could exceed 100% because of layering).

We calculated diversity using Shannon's Index (H') (McCune & Grace 2002). In 2009, we sampled vegetation in twenty-four 0.25 m² quadrats within each chronosequence plot. Species-accumulation curves showed this sampling effort inadequately captured richness, so we sampled forty-five 0.5 m² quadrats in each chronosequence plot in 2010. In both years, leaf litter was collected from one 0.25 m² subplot within each soil sampling plot, dried, and weighed.

Soil Erosion

Erosion was assessed using the mesh bag method, with bags constructed using the same methods as Hsieh (1992). Within each soil sampling plot (Fig. 2), one mesh bag was flattened to bare ground for 1 week in July 2009 during a period of intense thunderstorms. Bags were deployed again in August 2009 and kept in place longer, until November, due to a lack of strong storm events. Collected bags were dried and soil scraped from the bags was weighed.

Soil Respiration

Soil CO₂ efflux was measured using the base-trap respirometer method (Zilbiliske 1994), a chamber method that involves reaction of respired CO₂ with NaOH in suspended vials. One respirometer was deployed within each soil subplot (Fig. 2) on four occasions in 2009 (three times in July and once in October) and five occasions in 2010 (late June through July). Respirometers consisted of bottomless, white plastic chambers, capped on top and set into cylindrical plastic collars in the soil. For all 2009 sampling dates, respirometers were constructed of 10-cm diameter PVC (92-cm² footprint). For fall 2009 and all 2010 dates, respirometers were constructed from 19-L polyethylene pails (591 cm²) to reduce variance associated with spatial heterogeneity (Davidson et al. 2002). For each sampling event, collars were inserted ≥ 48 hours in advance into locations within plots containing representative cover and respirometers were deployed for approximately 24 hours.

Soil Organic Matter

Soil samples were collected from either six (2009) or five (2010) 10-m \times 10-m subplots systematically distributed within each chronosequence plot (Fig. 2). Four 1.3-cm diameter, 20-cm deep soil cores were collected from four quadrants within each subplot. Three cores in each group were composited for SOM analyses while the fourth was used to determine bulk density (Robertson et al. 1999).

Particle size of SOM is related to recalcitrance and thus the residence time of C ($\geq 50\%$ of SOM, Schulten & Schnitzer 1997), with finer size fractions persisting longer. Carbon in coarse particulate organic matter (POM) is typically mineralized within less than 1–10 years, whereas C in fine, mineral-associated SOM (maSOM) can persist for hundreds of years (Gregorich et al. 2006; Scharenbroch & Bockheim 2008).

We determined organic matter concentrations by mass loss on ignition (LOI) following particle size fractionation (Elliott & Cambardella 1991; Gregorich et al. 2006). Homogenized soil samples were passed through a 6-mm sieve, weighed, dried at 105°C for 24 hours, reweighed for determination of gravimetric soil moisture, and shaken for 15 hours with sodium hexametaphosphate. Samples were then sieved into fractions containing litter, coarse, and fine POM (IPOM: 2–6 mm, cPOM: 0.25–2.0 mm, and fPOM: 0.053–0.25 mm, respectively) and maSOM (<0.053 mm). Each fraction was dried, homogenized, and organic matter determined by LOI for 6 hours in a 360°C muffle furnace. Areal SOM stock was calculated using bulk density.

Data Analysis

Data from subplots were averaged at the chronosequence-plot level prior to performing statistical analyses. We tested for differences in tree BA and density between unrestored and restored plots with two-sided *t* tests. Understory composition was compared among restoration treatments by non-metric multidimensional scaling (NMDS). The nine vegetation quadrats associated with each of the five soil subplots per

chronosequence plot were aggregated. Species occurring in less than 5% of the resulting 35 sample units (5 subsamples in each of 7 chronosequence plots) were removed to avoid disproportionate effects of rare taxa (McCune & Grace 2002). To account for large differences in cover among species and plots, data were relativized by species and plot maxima. NMDS was based on Bray–Curtis dissimilarity using two axes. Differences by restoration status were tested by permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) performed using Bray–Curtis dissimilarity with 999 permutations and *p* values calculated by a Monte-Carlo procedure. We used indicator species analysis (ISA, Dufrêne & Legendre 1997) to identify species associated with areas of different restoration status. ISA evaluates the fidelity of species to groups; significance is tested by a Monte-Carlo procedure (McCune & Grace 2002).

We assessed ecosystem changes across the restoration chronosequence using regression. Time (in years) since restoration was the independent variable. The dependent variables analyzed were understory plant diversity and cover, litter mass, soil CO₂ flux, and total POM and maSOM. Variables were ln-transformed prior to analysis to meet distributional assumptions and increase homoscedasticity; ln-transformation also improved model fit based on AIC. We had insufficient data for a chronosequence analysis of soil erosion and instead contrasted results from restored and unrestored areas, assessing significance with a Wilcoxon rank-sum test, a nonparametric alternative to a *t* test for nonnormal data (Crawley 2007).

All statistical analyses were performed in R 2.10.1 (R Development Core Team 2009; Oksanen et al. 2010; Roberts 2010), with $\alpha < 0.10$ indicating significant results.

Results

Plant Community Structure

Unrestored canopies were dominated by buckthorn and *Fraxinus pennsylvanica* (green ash), with lesser amounts of *Ulmus americana* (American elm) and six other species (Table 1). In restored areas, 14 tree species were found, the most abundant being *Carya ovata* (shagbark hickory) and *Quercus alba* (white oak). Trees in unrestored areas were smaller-stemmed (mean BA \pm SE, unrestored: 137 \pm 16 cm, restored: 296 \pm 40; *p* = 0.0003) but did not differ in stem density (unrestored: 507 \pm 52 stems ha⁻¹, restored: 440 \pm 68; *p* = 0.46). Because only the largest stem of multi-stemmed individuals was measured, and buckthorn has numerous stems originating low to the ground (Fig. 1a), our sampling underestimated stem density in unrestored areas. Buckthorn had an average of 5.2 \pm 0.6 stems at breast height in McDonald Woods (Umek unpublished data, 2005).

Understory plant composition varied by restoration age (Fig. 3). Plots that were unrestored and most recently restored (2010) were most similar to each other. The number of indicator species and proportion of native indicator species increased with restoration age, as did understory plant diversity and cover and litter mass (Fig. 4a–c).

Table 1. Importance percentages (mean \pm SE) of tree species in areas of different restoration status in McDonald Woods.

| Species | Year restored | | | |
|---|-----------------|-----------------|-----------------|-----------------|
| | 1996 | 2001 | 2003 | Unrestored |
| <i>Carya ovata</i> (shagbark hickory) | 29.3 \pm 16.9 | 24.8 \pm 14.3 | 21.2 \pm 12.3 | — |
| <i>Quercus alba</i> (white oak) | 47.6 \pm 27.5 | 0.9 \pm 0.5 | 26.6 \pm 15.4 | — |
| <i>Quercus rubra</i> (red oak) | 1.7 \pm 1 | 24.5 \pm 14.1 | 8.2 \pm 4.7 | 1.5 \pm 0.9 |
| <i>Ostrya virginiana</i> (ironwood) | 12.5 \pm 7.2 | 2.4 \pm 1.4 | 11.5 \pm 6.6 | — |
| <i>Tilia americana</i> (basswood) | 1 \pm 0.6 | 11.5 \pm 6.6 | 3.6 \pm 2.1 | 1.3 \pm 0.8 |
| <i>Ulmus americana</i> (American elm) | 3.3 \pm 1.9 | 3.5 \pm 2 | 3.5 \pm 2 | 7.9 \pm 4.6 |
| <i>Fraxinus pennsylvanica</i> (green ash) | — | 16.7 \pm 9.6 | — | 30.3 \pm 17.5 |
| <i>Fraxinus americana</i> (white ash) | — | 3.9 \pm 2.3 | 9.5 \pm 5.5 | 1.4 \pm 0.8 |
| <i>Quercus bicolor</i> (swamp white oak) | — | — | 15.8 \pm 9.1 | — |
| <i>Quercus ellipsoidalis</i> (northern pin oak) | 0.6 \pm 0.4 | 7.3 \pm 4.2 | — | — |
| <i>Fraxinus nigra</i> (black ash) | 3.3 \pm 1.9 | — | — | — |
| <i>Acer saccharum</i> (sugar maple) | — | 2.9 \pm 1.7 | — | — |
| <i>Quercus macrocarpa</i> (bur oak) | — | 1.6 \pm 0.9 | — | — |
| <i>Crataegus</i> spp. (hawthorn) | 0.6 \pm 0.3 | — | — | 3.1 \pm 1.8 |
| <i>Juglans nigra</i> (black walnut) | — | — | — | 3 \pm 1.7 |
| <i>Prunus serotina</i> (black cherry) | — | — | — | 1.7 \pm 1 |
| <i>Rhamnus cathartica</i> (common buckthorn) | — | — | — | 49.7 \pm 28.7 |

Ecosystem Measures

More soil was trapped by erosion bags in unrestored than restored areas during mid-summer 2009 sampling (mean \pm SE, unrestored: 416 \pm 189 g/m², restored: 123 \pm 21; $p = 0.027$). The pattern was the same but nonsignificant in late-summer 2009 (unrestored: 121 \pm 40 g/m², restored: 62 \pm 10; $p = 0.135$). Soil CO₂ efflux differed between sampling years ($p < 0.0001$, note differences in timing of sampling and respirometer design), but in both years, efflux increased with restoration age at similar rates (Fig. 4d). There was modest evidence that SOM increased with restoration age (Fig. 4e & f), but unexplained variance was high. Increases in total POM were driven by maSOM; no other fractions significantly responded ($p = 0.37\text{--}0.98$).

Discussion

Ecosystem services are commonly cited in support of restoration. However, their provision is often not quantified and restoration is largely evaluated with vegetation-based indicators of structure (Ruiz-Jaen & Aide 2005b; Aronson et al. 2010). In this study, there were ecosystem changes associated with plant-community change in a previously buckthorn-invaded oak woodland. Restoration produced a tree canopy more characteristic of oak woodland and plant diversity, cover, and litter mass increased in the understory with restoration age. Restoration of vegetation was associated with lower rates of soil erosion but higher rates of soil CO₂ efflux. There was modest evidence of increasing SOM storage with restoration age. Caveats to this study include the small sample size and a lack of pre-restoration data and suitable reference sites.

Canopy opening following buckthorn removal facilitated restoration of understory vegetation. This was likely due to

increased light and perhaps belowground biotic interactions, e.g. shifts in dominant vegetation can promote mycorrhizal networks facilitating other plant species (van der Heijden & Horton 2009). While composition of understory vegetation varied among restored areas, diversity and cover increased with restoration age. Development of the understory community increased potential for plants to capture atmospheric C and transfer it to SOM, a function often associated with open, herbaceous habitats like grasslands and wetlands (Baer et al. 2002; Bridgman et al. 2006). Understories of healthy oak woodlands can also promote C sequestration through interactions between fine roots and soil (De Deyn et al. 2008) and accrual of recalcitrant litter (Martens 2000), which increased with restoration age, and reduced erosion through the presence of architecturally complex vegetation and litter. Litter increased with restoration despite temporary litter removal from prescribed fire, which only occurred in restored areas. Burning consisted of surface not ground fires and was followed by 4–5 year recovery time, making it unlikely that large amounts of SOM were consumed (Phillips et al. 2000).

We predicted that soil CO₂ efflux would decrease with restoration but found the opposite pattern. In retrospect, this is consistent with increased POM with restoration providing more substrate for mineralization (Robertson et al. 1999). While the trend of efflux increasing with restoration age was significant, the magnitude of change across the chronosequence was relatively small. However, soil respiration is heterogeneous, and our sampling intensity was insufficient for thoroughly characterizing CO₂ dynamics (Robertson et al. 1999; Davidson et al. 2002).

Another factor may have reduced SOM stock in buckthorn-dominated plots. Earthworms, which are non-native throughout the glaciated Midwest, were positively associated with buckthorn at this study site (Heneghan et al. 2007) and elsewhere (Madritch & Lindroth 2009). Earthworms disrupt soil

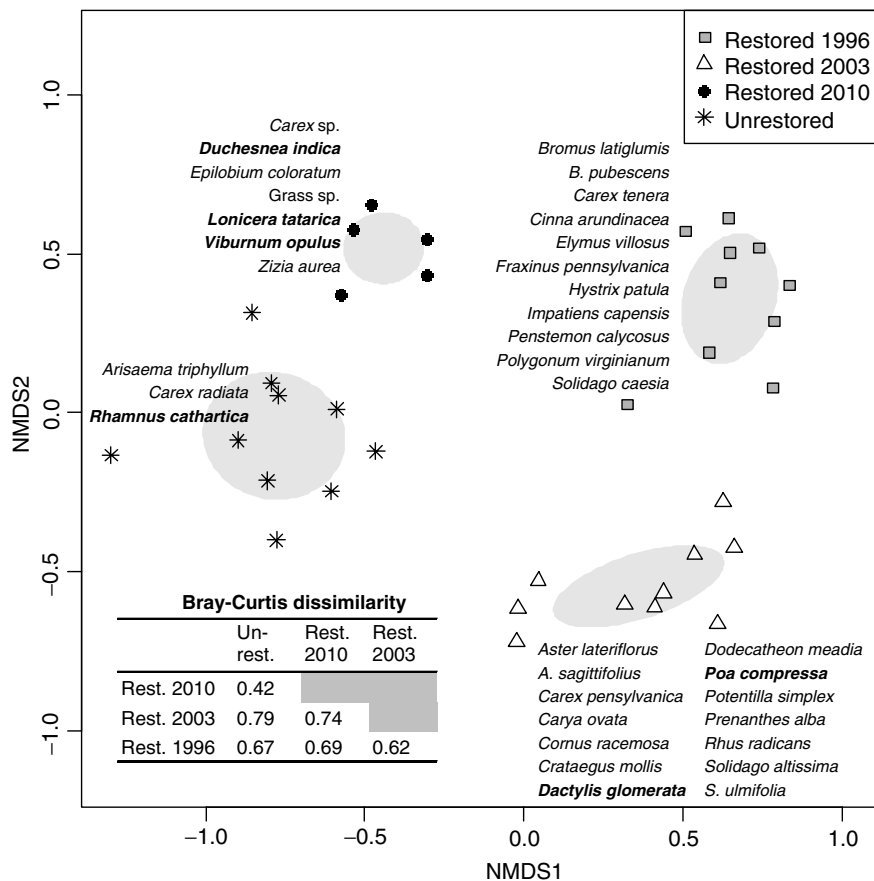


Figure 3. NMDS ordination (two axes, stress = 0.2) and results of indicator-species analysis for understory plant-community composition in areas of different restoration status in McDonald Woods, summer 2010. Each symbol represents one of five subplots sampled within each chronosequence plot. Gray ellipses depict one SD around the centroid of each group. Dissimilarities between groups are shown on the bottom left. Understory composition significantly differed by restoration status (PERMANOVA: $p < 0.001$). Species listed were significant indicators for their respective communities ($p < 0.05$); non-native species indicated in bold.

structure, reduce understory vegetation and litter, promote mineralization, and decrease SOM (Bohlen et al. 2004). Relatively low SOM in unrestored areas was likely due not just to buckthorn but a buckthorn-earthworm positive feedback (Heneghan et al. 2007).

Soil-C accumulation following restoration can be slow and unpredictable (Zedler & Callaway 1999). Brye and Kucharik (2003) did not find significant sequestration in Wisconsin prairies 25 years after conversion from agriculture. Similarly, longleaf pine restorations in Georgia had not yielded sequestration benefits 14 years post-reforestation (Markewitz et al. 2002). In restored wetlands, Craft et al. (2003) and Ballantine and Schneider (2009) found linear SOM increases but a failure to reach reference levels after 28 and 55 years, respectively.

Although SOM increased with restoration age, variance was high. McDonald Woods had not undergone the severe soil disturbances associated with cultivation, and thus may have been close to steady-state conditions prior to restoration (Gaudinski et al. 2000), making it more difficult to detect change. Nonetheless, we observed substantial, though weakly significant, SOM increases with restoration.

This study focused on maSOM due to its longer residence time, but removal of buckthorn could lower shorter-term C storage through loss of woody biomass. However, we found no support for such an effect. Allometric conversion of DBH data to aboveground biomass (Jenkins et al. 2004; Mascaro & Schnitzer 2011) showed that biomass per area was significantly higher in restored than unrestored areas and increased with restoration age (Gentile et al. 2009, unpublished data). Buckthorn may grow densely, but individuals are typically small and growth rates decline with size (Mascaro & Schnitzer 2011). In this study, only individuals of *Crataegus* spp. and *Ostrya virginiana* had lower mean biomass than buckthorn, while other species averaged 50% to 27 times higher biomass per individual. Mascaro and Schnitzer (2011) found similar patterns in 16 forest sites, where buckthorn-dominated stands had only half the biomass and annual biomass addition that was found in native-dominated stands. These results belie the notion that buckthorn might enhance C storage through rapid formation of thickets.

Other shrub or small-tree invasions have similar consequences. In systems as disparate as temperate-U.S. deciduous

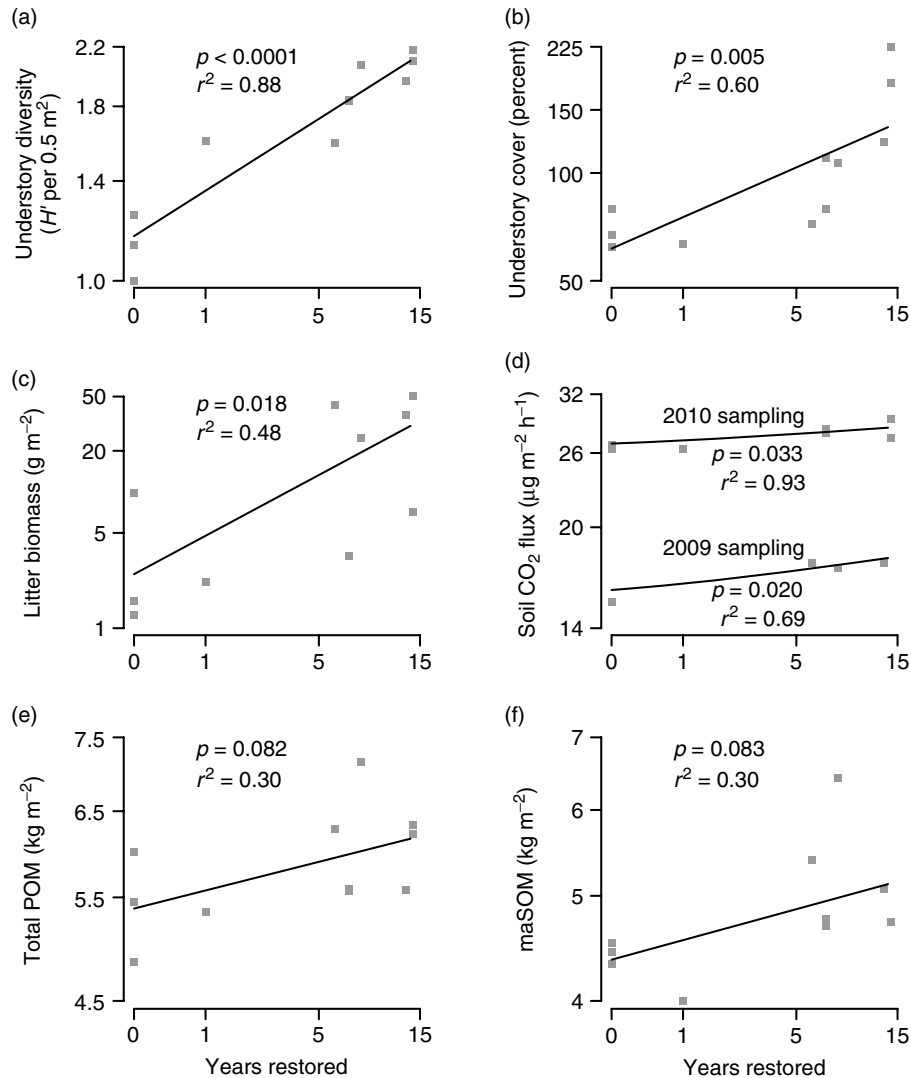


Figure 4. Regressions of community and ecosystem variables by restoration age (with unrestored plots as year 0). (a) Understory diversity: $\ln(y) = 0.151 + 0.220 \times \ln(x + 1)$. (b) Understory cover: $\ln(y) = 4.119 + 0.291 \times \ln(x + 1)$. (c) Litter mass: $\ln(y) = 0.913 + 0.934 \times \ln(x + 1)$. (d) Soil CO_2 flux, 2009 data: $\ln(y) = 2.736 + 0.055 \times \ln(x + 1)$, 2010 data: $\ln(y) = 3.272 + 0.027 \times \ln(x + 1)$. (e) Total POM: $\ln(y) = 1.683 + 0.051 \times \ln(x + 1)$. (f) Mineral associated SOM: $\ln(y) = 1.474 + 0.060 \times \ln(x + 1)$.

forests, Hawaiian tropical forests, and Argentinean semiarid habitats, woody invasions are associated with depauperate understory vegetation, suppression of native-species recruitment, rapid decomposition, and increased nutrient-cycling rates (Ehrenfeld et al. 2001; Allison & Vitousek 2004; Hoyos et al. 2010). Woody invasives may generally have stronger C-cycling effects than herbaceous invaders (Liao et al. 2008). Thus, the patterns we observed may be part of a broader phenomenon. If so, further research is needed to determine the extent to which ecological restoration can mitigate such effects.

Removal of buckthorn and active restoration of a degraded oak woodland benefited plant diversity. It also generally resulted in ecosystem changes indicative of greater C-storage potential. While habitat restoration in the upper Midwest may

have little potential to meaningfully offset fossil-fuel emissions (Fissore et al. 2010; but see Lal et al. 2011), it can provide substantial benefits to site-level ecosystem function.

Implications for Practice

- Restoration of oak-woodland understory vegetation after buckthorn removal may promote ecosystem changes associated with carbon storage.
- Observed ecosystem changes came after what were not just one-time restoration actions but restoration followed by years of ongoing, active management.
- Measurement and communication of enhanced ecosystem services associated with restoration can strengthen and broaden support for restoration efforts.

Acknowledgments

Funding came from NSF REU Site grant DBI-0648972. We thank College First students A. Lane and K. Altantulkhuur for work in the field and laboratory, B. Scharenbroch for assistance with soil analyses, and S. Still for GIS help. Comments by S. Baer and two anonymous reviewers greatly improved the manuscript.

LITERATURE CITED

- Allison, S. D., and P. M. Vitousek. 2004. Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. *Oecologia* **141**:612–619.
- Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**:32–46.
- Aronson, J., J. N. Blignaut, S. J. Milton, D. Le Maitre, K. J. Esler, A. Limouzin, et al. 2010. Are socioeconomic benefits of restoration adequately quantified? A meta-analysis of recent papers (2000–2008) in *Restoration Ecology* and 12 other scientific journals. *Restoration Ecology* **18**:143–154.
- Baer, S. G., D. J. Kitchen, J. M. Blair, and C. W. Rice. 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. *Ecological Applications* **12**:1688–1701.
- Ballantine, K., and R. Schneider. 2009. Fifty-five years of soil development in restored freshwater depressional wetlands. *Ecological Applications* **19**:1467–1480.
- Bohlen, P. J., P. M. Groffman, T. J. Fahey, M. C. Fisk, E. Suarez, D. M. Pelletier, and R. T. Fahey. 2004. Ecosystem consequences of exotic earthworm invasion of north temperate forests. *Ecosystems* **7**:1–12.
- Bridgham, S. D., J. P. Megonigal, J. K. Keller, N. B. Bliss, and C. Trettin. 2006. The carbon balance of North American wetlands. *Wetlands* **26**:889–916.
- Brye, K. R., and C. J. Kucharik. 2003. Carbon and nitrogen sequestration in two prairie topochronosequences on contrasting soils in southern Wisconsin. *American Midland Naturalist* **149**:90–103.
- Craft, C., P. Megonigal, S. Broome, J. Stevenson, R. Freese, J. Cornell, L. Zheng, and J. Sacco. 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecological Applications* **13**:1417–1432.
- Crawley, M. 2007. *The R Book*. Wiley, West Sussex, England.
- Curran, P., D. Smedley, P. Thompson, and A. T. Knight. 2012. Mapping restoration opportunity for collaborating with land managers in a carbon credit-funded restoration program in the Makana Municipality, Eastern Cape, South Africa. *Restoration Ecology* **20**:56–64.
- Davidson, E. A., K. Savage, L. V. Verchot, and R. Navarro. 2002. Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology* **113**:21–37.
- De Deyn, G. B., J. H. C. Cornelissen, and R. D. Bardgett. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters* **11**:516–531.
- Dufrène, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**:345–366.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**:503–523.
- Ehrenfeld, J. G., P. Kourtev, and W. Z. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* **11**:1287–1300.
- Elliott, E. T., and C. A. Cambardella. 1991. Physical separation of soil organic-matter. *Agriculture, Ecosystems and Environment* **34**:407–419.
- Fissore, C., J. Espeleta, E. A. Nater, S. E. Hobbie, and P. B. Reich. 2010. Limited potential for terrestrial carbon sequestration to offset fossil-fuel emissions in the upper midwestern US. *Frontiers in Ecology and the Environment* **8**:409–413.
- Galatowitsch, S. M. 2009. Carbon offsets as ecological restorations. *Restoration Ecology* **17**:563–570.
- Gaudinski, J. B., S. E. Trumbore, E. A. Davidson, and S. H. Zheng. 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. *Biogeochemistry* **51**:33–69.
- Gregorich, E. G., M. H. Beare, U. F. McKim, and J. O. Skjemstad. 2006. Chemical and biological characteristics of physically uncomplexed organic matter. *Soil Science Society of America Journal* **70**:975–985.
- Hansson, L. A., C. Bronmark, P. A. Nilsson, and K. Abjornsson. 2005. Conflicting demands on wetland ecosystem services: nutrient retention, biodiversity or both? *Freshwater Biology* **50**:705–714.
- Heneghan, L., C. Rauschenberg, F. Fatemi, and M. Workman. 2004. European buckthorn (*Rhamnus cathartica*) and its effects on some ecosystem properties in an urban woodland. *Ecological Restoration* **22**:275–280.
- Heneghan, L., F. Fatemi, L. Umek, K. Grady, K. Fagen, and M. Workman. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in Midwestern US woodlands. *Applied Soil Ecology* **32**:142–148.
- Heneghan, L., J. Steffen, and K. Fagen. 2007. Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: Impact on leaf litter decomposition. *Pedobiologia* **50**:543–551.
- Hoyos, L. E., G. I. Gavier-Pizarro, T. Kuemmerle, E. H. Bucher, V. C. Radeloff, and P. A. Tecco. 2010. Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the Sierras Chicas of Crdoba, Argentina. *Biological Invasions* **12**:3261–3275.
- Hsieh, Y. P. 1992. A mesh-bag method for field assessment of soil erosion. *Journal of Soil and Water Conservation* **47**:495–499.
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. USDA Forest Service, Newton Square, Pennsylvania.
- Knight, K. S., J. S. Kurylo, A. G. Endress, J. R. Stewart, and P. B. Reich. 2007. Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review. *Biological Invasions* **9**:925–937.
- Lal, R., J. A. Delgado, P. M. Groffman, N. Millar, C. Dell, and A. Rotz. 2011. Management to mitigate and adapt to climate change. *Journal of Soil and Water Conservation* **66**:276–285.
- Liao, C. Z., R. H. Peng, Y. Q. Luo, X. H. Zhou, X. W. Wu, C. M. Fang, J. K. Chen, and B. Li. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *The New Phytologist* **177**:706–714.
- Madritch, M. D., and R. L. Lindroth. 2009. Removal of invasive shrubs reduces exotic earthworm populations. *Biological Invasions* **11**:663–671.
- Markewitz, D., F. Sartori, and C. Craft. 2002. Soil change and carbon storage in longleaf pine stands planted on marginal agricultural lands. *Ecological Applications* **12**:1276–1285.
- Martens, D. A. 2000. Plant residue biochemistry regulates soil carbon cycling and carbon sequestration. *Soil Biology and Biochemistry* **32**:361–369.
- Mascaro, J., and S. A. Schnitzer. 2011. Dominance by the introduced tree *Rhamnus cathartica* (common buckthorn) may limit aboveground carbon storage in Southern Wisconsin forests. *Forest Ecology and Management* **261**:545–550.
- McCune, B., and J. B. Grace. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, Oregon.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, R. G. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2010. *vegan: Community ecology package*. R package version 1.17-0.
- Phillips, D. H., J. E. Foss, E. R. Buckner, R. M. Evans, and E. A. FitzPatrick. 2000. Response of surface horizons in an oak forest to prescribed burning. *Soil Science Society of America Journal* **64**:754–760.
- Development Core Team, R. 2009. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ricketts, T. H., E. Dinerstein, D. M. Olson, C. J. Loucks, W. Eichbaum, D. DellaSala, et al. 1999. *Terrestrial ecoregions of North America: a conservation assessment*. Island Press, Washington, D.C.
- Rieman, B. E., P. F. Hessburg, C. Luce, and M. R. Dare. 2010. Wildfire and management of forests and native fishes: conflict or opportunity for convergent solutions? *BioScience* **60**:460–468.

- Roberts, D. W. 2010. labdsv: Ordination and multivariate analysis for ecology. R package version 1.4-1.
- Robertson, G. P., D. C. Coleman, C. S. Bledsoe, and P. Sollins. 1999. Standard soil methods for long-term ecological research. Oxford University Press, New York.
- Ruiz-Jaen, M. C., and T. M. Aide. 2005a. Restoration success: how is it being measured? *Restoration Ecology* **13**:569–577.
- Ruiz-Jaen, M. C., and T. M. Aide. 2005b. Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. *Forest Ecology and Management* **218**:159–173.
- Scharenbroch, B. C., and J. G. Bockheim. 2008. Gaps and soil C dynamics in old growth northern hardwood-hemlock forests. *Ecosystems* **11**:426–441.
- Schulten, H. R., and M. Schnitzer. 1997. Chemical model structures for soil organic matter and soils. *Soil Science* **162**:115–130.
- Swingland, I. 2002. Capturing carbon & conserving biodiversity: the market approach. Earthscan Publications, London, United Kingdom.
- van der Heijden, M. G. A., and T. R. Horton. 2009. Socialism in soil? The importance of mycorrhizal fungal networks for facilitation in natural ecosystems. *Journal of Ecology* **97**:1139–1150.
- Yates, E. D., D. F. Levia, and C. L. Williams. 2004. Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. *Forest Ecology and Management* **190**:119–130.
- Zedler, J. B. 2003. Wetlands at your service: reducing impacts of agriculture at the watershed scale. *Frontiers in Ecology and the Environment* **1**:65–72.
- Zedler, J. B., and J. C. Callaway. 1999. Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restoration Ecology* **7**:69–73.
- Zilbiliske, L. M. 1994. Carbon mineralization. in R. W. Weaver, S. Angle and S. Bottomley, editors. *Methods of soil analysis. Part 2. Microbiological and biochemical properties*. Soil Science Society of America, Madison, Wisconsin.