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Forest micro-environment develops through time: Changes in physical and structural heterogeneity follow abandonment from two forms of agriculture

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ABSTRACT

Agriculture alters and homogenizes the physical environment, and persistent changes potentially affect community development in post-agricultural forests. We ask whether physical and structural development differs between second-growth stands of contrasting ages and agricultural histories. Formerly cultivated and pastured sites were expected to follow separate trajectories of succcessional development but eventually to converge as natural processes obscured the environmental legacies of agriculture. We used a replicated chronosequence to examine microenvironment development in successional stands over 80 years following canopy closure and compared successional stands with a control group of long-established stands. Physical, edaphic, and structural variables were measured in each site. Microtopography increased through successional time, while canopy openness and soil bulk density declined. Formerly cultivated sites showed less microtopographic variation and higher bulk density than pastured sites, consistent with a history of plowing. Formerly cultivated sites showed spatial homogenization in microtopography, soil organic matter, and herb cover. Stands in the 61–80 year age class did not differ significantly from long-established forest in any of the environmental variables or the spatial distribution of such variation. Our results suggest that 80 years of forest development is sufficient for most environmental legacies of agriculture to fade, reducing their potential to influence plant community composition. However, contrasting land-use history is still evident for several decades and may contribute to community structure over that period.

1. Introduction

Most deciduous forest in eastern North America and northern Europe has regenerated after abandonment from agriculture in the 20th century (Williams, 1989; Hermy and Verheyen, 2007). Agricultural activities result in alterations to the ground surface and upper layers of soil that may persist in successional forest communities following abandonment (Flinn and Marks, 2007). The physical and chemical legacy of agriculture has been shown to last decades or longer in some studies (Koerner et al., 1997; Verheyen et al., 1999; Dupouey et al., 2002), and physical structure may be reflected in second-growth forest vegetation (Flinn, 2007; Gilbert and Lechowicz, 2004). Because most deciduous forests in eastern North America and northern Europe are less than a century old, the majority of modern forest is likely to show some form of agricultural influence. Thus, an understanding of agricultural legacies is essential for managing diversity. In this study, we use a series of sites of varying age (a "chronosequence") to examine physical and structural development in successional stands abandoned from agriculture in the mid- and late- twentieth century.

Agricultural soils typically have a higher bulk density, higher pH, higher nutrient content, and lower organic content than undisturbed sites nearby (Davidson and Ackerman, 1993; Robertson et al., 1993; Compton et al., 1998; Compton and Boone, 2000). After abandonment, soil pH typically declines as a natural plant community develops and root exchange increases hydrogen ion concentration (Verheyen et al., 1999; Ritter et al., 2003). Soil organic matter increases as the successional community decomposes (Verheyen et al., 1999; Flinn and Marks, 2007). Soil bulk density is reduced by root penetration and by the activity of burrowing animals, although bulk density is likely to remain high long after forest establishment (Messing et al., 1997).

Stand growth both drives and responds to changes in the physical environment following abandonment. Canopy openness may be patchy during the colonization phase, but decreases as individual trees grow and canopies merge (Holmes and Matlack, 2017). The canopy becomes heterogenous again as individual trees mature and local disturbance allows light to reach the forest floor (Oliver and Larson, 1996). Herbs and shrubs typically respond to canopy openness, and dense populations of shade-intolerant species are common in early successional

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communities with abundant light (Swanson et al., 2010).

Litter cover increases as individual trees grow, reflecting both the production and decomposition rates of leaves (Facelli and Pickett, 1991). Long-established forest typically has higher values of litter cover and depth than successional stands (Facelli and Carson, 1991) and greater abundance of coarse woody debris on the forest floor (Sturtevant et al., 1997). Woody debris coincides with large tree mortality and development of canopy gaps in long-established forests (Franklin et al., 1981), suggesting a nonlinear schedule of debris accumulation. Each of these environmental parameters potentially shapes the plant community in the developing forest.

1.1. Spatial heterogeneity

Agriculture imposes physical homogeneity by removing vegetation, leveling the ground surface, and mixing the soil (Vellend et al., 2007), a condition which persists into successional stands following abandonment. Forest herb and shrub species are sensitive to fine-scale physical variation in both long-established (Gilbert and Lechowicz, 2004; Burton et al., 2011) and successional stands (Hougen and Matlack, 2012), implying that fine-scale physical heterogeneity supports diversity and generates spatial heterogeneity in forest communities. If availability of suitable microsites facilitates colonization of a successional stand, then assembly of a forest community is potentially limited by the processes and rates by which regeneration microsites become available (Flinn, 2007).

Microsite heterogeneity may arise through a variety of biological and physical processes. Spatial distribution and growth rates of woody colonizers potentially create variation in canopy openness in early successional sites (Holmes and Matlack, 2017). In older stands microtopographic variation and canopy openness are created by uprooting of trees (Beatty, 1984). Formation of pit-and-mound microtopography typically coincides with the deaths of large trees as stands mature (Oliver and Larson, 1996; Flinn and Marks, 2007). Microtopography may also be influenced by burrowing animals, root penetration, and erosion. Heterogeneous soil surfaces are typical of long-established forests (Flinn and Marks, 2007; Wessels, 2010).

1.2. Forms of agriculture

Cultivation and pasturing, two historically common forms of agriculture in eastern North America, leave contrasting legacies in post-agricultural forests. Cultivation removes most surface irregularity and mixes the soil. A level, homogeneous soil surface is a strong indicator of former cultivation, potentially persisting long after development of a closed-canopy forest. Cultivation disrupts the microstructure of soils leading to high bulk density and low porosity (Oades, 1993), a condition that persists in formerly plowed sites (Compton et al., 1998). Cultivation reduces soil organic content by increasing both mineralization and erosion of carbon (Davidson and Ackerman, 1993; Robertson et al., 1993). Soil amendments in row cropping elevate soil pH and nutrient content (Flinn and Marks, 2007), and nutrient distributions become increasingly homogeneous with increasing intensity of land use (Fraterrigo et al., 2005; Flinn and Marks, 2007).

In contrast to cultivation, pasturing does not involve dramatic chemical or mechanical alterations to soil. Formerly pastured sites are typically lower in pH, cation concentration, and bulk density than cultivated sites (Koerner et al., 1997; Wilson et al., 1997; Falkengren-Gerup et al., 2006) and higher in organic content (Duiker, 2004). Although both cultivation and pasturing leave legacies of homogenization in the physical environment, pasturing allows some amount of the original microsite variation to remain, and forest species may persist at low levels in the pasture matrix (Bellemare et al., 2002).

After abandonment, both pastured and cultivated sites undergo a process of physical development in which they become more structurally and edaphically similar to long-established forest. However, the incremental progress of development has rarely been documented, and it is not clear how long the initial distinction between cultivated and pastured sites persists. Most previous studies have used binary comparisons of successional and long-established stands rather than considering incremental change through time, and, thus, say little about the temporal scale of forest development.

The flexibility of pedogenic processes (Targulian and Krasilnikov, 2007) and the observed development of forest communities on denuded land following the last ice age (Davis, 1983) suggest that the physical environment of all post-agricultural sites will eventually converge on the condition of long-established forest. However, the rates of site development for pastured and cultivated sites are unknown. Indeed, considering the extremely long time scale of soil development relative to the scale of plant life histories (e.g. Robertson et al., 1993; Targulian and Krasilnikov, 2007), it is not clear whether post-agricultural stands can be interpreted as converging, at all.

We documented structural and edaphic development in second-growth stands spanning eighty years following canopy closure. We ask how rapidly post-agricultural sites approach long-established forest conditions, if indeed they do, and whether specific agricultural practices leave recognizable legacies in the successional forest. As a null hypothesis, we predict that the multivariate physical and biotic structure of post-agricultural forests changes incrementally through successional time consistent with previous studies based on binary comparisons and individual variables. Because cultivation and pasturing represent different successional starting points, we suggest that rates of site development will differ between the two land-use histories.

2. Methods

We described the physical, edaphic, and structural environment at forest sites in Athens, Morgan, and Perry Counties in Southeastern Ohio, USA (39°9′ to 39°34′N, and 81°54′ to 82°03′W). All sites were located in the unglaciated Marietta section of the Allegheny Plateau (Brockman, 1998), a highly eroded peneplain characterized by low ridges and small, steep-sided valleys. Soils are well-drained silt and sandy loams derived from Pennsylvanian parent material (Lucht et al., 1985). Natural vegetation is a mixed deciduous forest belonging to Braun's (1950) Mixed Mesophytic association. Heterogeneity in slope, exposure, and disturbance supports a diverse herb and shrub flora (Harrelson and Cantino, 2006). Canopy dominants include *Quercus* spp., *Carya* spp., and *Acer* spp., with *Platanus occidentalis* common on floodplains, and *Liriodendron tulipifera* prominent in disturbed areas.

Extensive forest clearance began in the early 1800′s with the arrival of European settlers. Clearance occurred in a piecemeal fashion as small parcels were cut for subsistence farming, resulting in only 10–20% forest cover remaining in the early 20th century (Williams, 1989). Most agricultural land was abandoned in the early- to mid-20th century in response to a nationwide decline in agricultural prices and the growing availability of industrial jobs in nearby cities. As a result, most modern forest is younger than 100 years, with a structure and flora typical of early successional sites. Second growth communities show an increase in basal area through successional time, a decrease in stem density, and a decline in light-demanding tree species, although long-lived pioneer species such as *Liriodendron tulipifera* and *Acer saccharum* can persist for a century or more (Holmes and Matlack, 2017).

2.1. Site selection

Historically, steep slopes and irregular ridge-tops were used for pastures or wood lots, whereas floodplains and level sites were preferred for cultivation (Weinfurtner, 2002). This creates an interaction of land use and topography that confounds environmental and anthropogenic variation in modern forests and often complicates studies of land-use effects (Flinn et al., 2005). In order to minimize the influence of topography and focus our analysis on land-use legacies, we