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Biogeographic synthesis of secondary succession rates in eastern North America

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ABSTRACT

Aim Mechanistic models of old-field plant succession have generally lacked a broader biogeographic context in which climate, soils and species pools could play a significant role in mediating succession rates. We examine broad-scale patterns in old-field succession and introduce a hierarchical conceptual model to incorporate potential mechanisms operating at multiple spatial scales.

Location We reviewed secondary succession studies across the Eastern Deciduous Forest (EDF) of North America.

Methods We collected data from all published studies that reported the time necessary for woody species to reach either 10% or 50% cover in old-field systems throughout the EDF. We used regression approaches to determine whether rates of succession are controlled by climatic and edaphic factors that vary at broad spatial scales.

Results We found that the rate at which woody species colonize and dominate old fields decreases significantly with latitude. Rates of woody succession were highly correlated with both annual temperature (growing degree-days for years to 10% and 50% cover) and measures of soil fertility (cation exchange capacity and reported pre-agroindustrial (1930) maize yields for years to 10% cover), all of which show a significant latitudinal trend across the EDF.

Main conclusions We suggest that the driver of this pattern is geographic variation in the intensity of competition between herbaceous and woody species, which we relate to the effects of (1) temperature regime, (2) edaphic factors related to soil fertility, and (3) plant traits, which may vary latitudinally in response to climate and edaphic factors. Although insufficient data exist to evaluate the relative importance of these factors, we argue that research in this area is necessary to gain an understanding of how future landscapes will be affected by global climate and land use change.

Keywords

Eastern Deciduous Forest, growth rate, North America, plant traits, soil fertility, succession, temperature, USA, woody plants.

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INTRODUCTION

In the Eastern Deciduous Forest (EDF) of North America, over a century of studies of secondary succession has produced a standard descriptive model of the transition of croplands to forest, namely colonization by annual herbs, followed by dominance by perennial herbs and grasses, and subsequent

stages of woody species colonization and dominance (Oosting, 1942; Keever, 1950; Bazzaz, 1963). Additional studies from Europe (Bornkamm, 1988) and Japan (Numata & Yamai, 1955; Hayashi, 1977) show that this pattern is widespread in temperate areas where agricultural practices do not significantly alter the abiotic environment (Cramer *et al.*, 2008). Although the general pattern of compositional shifts is

consistent across a broad geographic range, the rate at which these changes occur can be highly variable (Bazzaz, 1968). A large number of possible mechanisms have been proposed as regulators of the rate of succession, including herbivory (McBrien *et al.*, 1983; Gill & Marks, 1991; Ostfeld & Canham, 1993), previous land use history (Golley & Gentry, 1965; Cramer *et al.*, 2008) and dispersal limitation (Billings, 1938; Oosting, 1942; Bard, 1952; Bormann, 1953; Bazzaz, 1968; Buell *et al.*, 1971; Myster & Pickett, 1992). To date, however, there have been few efforts to build a synthetic model to explain broad-scale variation in the rates of succession.

The lack of a general model for successional rates limits our ability to predict how changes in drivers of ecological processes, such as climate change and eutrophication, will impact future ecosystems. In particular, the rate at which woody species become dominant over early successional herbaceous species represents a critical transition in ecosystem development. For a given plant community, the relative abundance of herbaceous versus woody vegetation is well recognized as one of the major regulators of ecosystem properties, including processes such as carbon sequestration (Breshears, 2006; Galang *et al.*, 2007), productivity and nutrient cycling (Mellinger & McNaughton, 1975; Inouye *et al.*, 1987) and water balance (Jackson *et al.*, 2005), as well as of community attributes such as species diversity (Mellinger & McNaughton, 1975; Harpole & Tilman, 2006), trophic structure (Inouye *et al.*, 1987; Haddad *et al.*, 2001) and invasive species colonization (Rejmánek *et al.*, 2005).

Furthermore, anecdotal evidence suggests that the rate at which woody species become dominant after field abandonment varies significantly across the range of the EDF. Early studies in the south-eastern piedmont region indicated very fast transitions from abandoned field to closed-canopy forest (McQuilken, 1940; Oosting, 1942; Keever, 1950), in some cases proceeding in less than a decade (Keever, 1950). Subsequent researchers noted the generally slower rates of woody encroachment in mid-western (Patzger & Patzger, 1950; Quarterman, 1957; Bazzaz, 1968) and northern (Bard, 1952; Mellinger & McNaughton, 1975; Inouye *et al.*, 1987) locations. However, geographic patterns in the rate of woody establishment after field abandonment have never been systematically evaluated. This putative biogeographic variation in rates of succession suggests that factors operating at larger scales than those previously proposed (e.g. herbivory, land use history, dispersal limitation or proximity to seed source) may be important regulators of this ecological process.

Although an exhaustive review of mechanisms that might lead to a latitudinal gradient in rates of succession across the EDF is beyond the scope of this paper, we provide a brief summary of potential mechanisms as a means of focusing subsequent analysis of existing succession data. We then review studies of secondary succession addressing the rate at which woody species colonize and dominate abandoned agricultural fields across the EDF to quantify geographic patterns in rates of old-field succession, and determine the level of support for the

various mechanisms. We develop the hypothesis that the competitive intensity between herbaceous and woody species is related to climate and soil factors that show strong latitudinal variation in eastern North America, controlling both the overall interaction intensity between these major plant life forms and the composition of local species pools.

WHAT FACTORS COULD LEAD TO BROAD-SCALE VARIATION IN RATES OF SUCCESSION?

Dispersal limitation

Some early conceptual models (Egler, 1954) and subsequent research demonstrated that dispersal limitation can be a key determinant of the rate of succession. Proximity to and availability of seed sources have been shown to limit rates of tree invasion across the EDF, for example in North Carolina (Oosting, 1942; Bormann, 1953), Georgia (Billings, 1938), Illinois (Bazzaz, 1968) and New Jersey (Bard, 1952; Buell *et al.*, 1971; Myster & Pickett, 1992). Given that wind-dispersed seeds typically have longer average dispersal distances than animal-dispersed seeds (Baskin & Baskin, 1998), regional variation in the dominant dispersal mode of old-field colonizers could lead to broad-scale patterns in the rate of succession.

A related potential control on the rate of succession is the size of the original forest clearance. Golley & Gentry (1965) suggested that a large enough field essentially halted succession, although a recent study (Robinson *et al.*, 1995) found no effect of patch size on rate of succession for relatively small fields. Furthermore, based on data from the US Agricultural Census of 1950 (USDA, 1952), average farm size did not differ between states in the Southeast (mean across states, 113 acres, SD 64.2; see Table 1 for a list of states in each region), Northeast (115, 40.5), Mid-Atlantic (98, 20) or Midwest (126, 22.9). Although this does not provide direct information on the size of farms abandoned across the latitudinal gradient, it at least suggests that there were not large systematic differences in the size of farms during the period when many fields were abandoned. However, given the clear differences in topography throughout the EDF, it seems likely that different regions may have different sizes and shapes of fields, which could contribute to variation in rates of succession both at local and at regional scales.

Land use history

Another key factor that can affect rates of succession is the nature of the agricultural disturbance. Cramer *et al.* (2008) argued that variation in the intensity of agricultural disturbance can determine the trajectory of recovery during succession, ranging from rapid recovery when minimal manipulations have occurred to the development of alternate stable states when significant modification was necessary for agriculture. The gradient of modification discussed by Cramer *et al.* (2008) is much broader than that which probably occurred throughout the EDF, where most of the landscape is

Table 1 Dispersal modes of the dominant species in early old-field succession in various regions of the Eastern Deciduous Forest of North America. The Northeast includes Connecticut (CT), Maine (ME), Massachusetts (MA), New Hampshire (NH), New York (NY), Rhode Island (RI) and Vermont (VT); the Midwest includes Arkansas (AR), Illinois (IL), Indiana (IN), Michigan (MI), Missouri (MO), Ohio (OH) and Wisconsin (WI); the Mid-Atlantic includes Delaware (DE), Maryland (MD), New Jersey (NJ) and Pennsylvania (PA); and the Southeast includes Alabama (AL), Florida (FL), Georgia (GA), Kentucky (KY), Louisiana (LA), Mississippi (MS), North Carolina (NC), South Carolina (SC), Tennessee (TN), Virginia (VA) and West Virginia (WV). Species that are important in more than one region are listed multiple times.

Region	Species	Dispersal mode
Northeast	<i>Betula</i> spp.	Wind
	<i>Cornus racemosa</i>	Animal
	<i>Fraxinus americana</i>	Wind
	<i>Pinus rigida</i>	Wind
	<i>Pinus strobus</i>	Wind
Midwest	<i>Acer negundo</i>	Wind
	<i>Cornus florida</i>	Animal
	<i>Diospyros virginiana</i>	Animal
	<i>Fraxinus americana</i>	Wind
	<i>Pinus banksiana</i>	Wind
	<i>Populus grandidentata</i>	Wind
	<i>Sassafras albidum</i>	Animal
<i>Ulmus rubra</i>	Wind	
Mid-Atlantic	<i>Acer rubrum</i>	Wind
	<i>Juniperus virginiana</i>	Animal
	<i>Prunus serotina</i>	Animal
	<i>Liquidambar styraciflua</i>	Animal
Southeast	<i>Celtis occidentalis</i>	Animal
	<i>Juniperus virginiana</i>	Animal
	<i>Liquidambar styraciflua</i>	Animal
	<i>Pinus echinata</i>	Wind
	<i>Pinus taeda</i>	Wind
	<i>Ulmus alata</i>	Wind

relatively favourable for agriculture. However, given the generally poorer soils in southern regions of the EDF (see below), lower latitudes are likely to have experienced greater modification. Thus, the hypothesis of Cramer *et al.* (2008) would predict slower rates of succession in these areas, rather than the faster rates of succession generally observed in the South (McQuilken, 1940; Oosting, 1942; Keever, 1950).

Herbivory

Herbivory has been demonstrated to play an important role in the rate of succession in a number of studies (McBrien *et al.*, 1983; Gill & Marks, 1991; Ostfeld & Canham, 1993). When herbivore density is high enough, particularly small mammal herbivores that specialize on browsing tree seedlings, seedling mortality rates can exceed 60% per year (Gill & Marks, 1991). However, studies that have looked at the intensity of herbivory

or herbivore biomass across latitudinal gradients have found either no trend (Andrew & Hughes, 2005) or increasing herbivore biomass at low latitudes (Crete, 1999). A recent study found that rates of insect herbivory on leaves of four forest tree species increased at lower temperatures across the EDF (Adams & Zhang, 2009). None of these studies looked specifically at rodent herbivore density, so we cannot rule out that the intensity of herbivory affects the latitudinal gradient in the rate of succession.

Climate

The latitudinal trend in temperature regime mirrors the change in rates of woody succession across the EDF. Given the central role that temperature plays in many biological and ecological processes, there are a number of mechanisms by which variation in climate could influence the rate at which woody species establish in old fields. In particular, the temperature regime could alter growth rates and growing season duration, either of which could promote woody dominance at the expense of herbaceous perennials. For example, evidence suggests that species in warmer climates should have greater potential net growth rates (Farnsworth *et al.*, 1995; Weston & Bauerle, 2007; Zhang & Dang, 2007). If this is the case, one would expect woody species in warmer climates to spend fewer growing seasons experiencing low light levels under a herbaceous canopy. In addition, the longer growing seasons in southern locales suggest that, all else being equal, woody species in warmer climates should have a greater annual height increment, even if growth is slowed by competition for light (Norby *et al.*, 2003). Thus, temperature-regime differences may be sufficient to promote the faster advance of woody species dominance at southern latitudes.

Soil nutrient availability

Herbaceous plants tend to have a higher physiological demand for mineral resources such as nitrogen, phosphorous and major cations than woody plants (Larcher, 2001). Thus, high-fertility environments should favour herbaceous dominants over woody seedlings (Graves *et al.*, 2006). Several studies have shown that early successional species resist invasion by later successional species under added nutrients, particularly nitrogen, although these studies were not looking explicitly at woody invaders (Carson & Barrett, 1988; McLendon & Redente, 1992). Thus, the balance of herbaceous–woody competition may lie in gross differences in tissue chemistry between these growth forms, and the rate of succession may vary according to broad geographic gradients of soil nutrient availability. The differences in soil fertility between glaciated and unglaciated soils can be dramatic (von Englen, 1914), and can have strong effects on plant performance (Bailey *et al.*, 2004). Thus, patterns of historical glaciations, and hence enhanced soil fertility in the north that favours herbaceous old-field dominants, may partly explain the latitudinal pattern in rates of woody succession.

Species traits related to competitive ability

Grime (2001) suggested a general framework in which plants from fertile, productive habitats ('competitors') often exhibit rapid lateral spread. This framework suggests that differences in soil fertility among sites influence herbaceous–woody competition by selecting for 'competitor' herb species that are able to quickly usurp available light and soil resources. This hypothesis is related to the soil nutrient status argument above, but is distinguished by its proximate mechanism of plant traits (e.g. clonal growth form) rather than differences in soil fertility alone that explain herbaceous versus woody species dominance. Old-field herbaceous assemblages throughout the EDF are often dominated by clonal *Solidago* species on fertile, fine-textured soils, and can be highly invasion-resistant where rhizomes are well developed (Gill & Marks, 1991).

Traits of woody species selected by local environments could also control the rate at which woody species become dominant over the course of succession. In areas experiencing significant frosts, trade-offs between competitive ability (e.g. annual growth) and survival (e.g. frost- and cold-tolerance traits) are likely (Körner & Renhardt, 1987; Woodward, 1987; Loehle, 1998; Green, 2005). If the colder climate in the northern range of the EDF has exerted a strong enough selective pressure for the development of frost resistance on the set of tree species most common in old-field succession, the resulting decrease in annual growth rate could be responsible for the slower rate of woody succession, independent of herb composition.

MATERIALS AND METHODS

We conducted a literature review with the objective of obtaining quantitative data on the rate at which woody species become established and dominate old fields after agricultural abandonment across the EDF, roughly from Maine and southern Ontario to Louisiana and northern Florida (Fig. 1). We screened the citations listed in a comprehensive bibliographic review of the subject (Rejmánek & Van Katwyk, 1991) spanning studies from 1901 to 1991, and augmented this information with online citation searches using the ISI Science Citation Index database up to mid-2006. We filtered these citations with the criteria that each study should: (1) be within the above geographic scope; and (2) contain a quantitative description of the timing of woody plant colonization and changes in abundance after field abandonment (from crop or pasture), with no continued disturbance, using either time series observations or chronosequences. Our measure of woody abundance was percentage cover of all woody vegetation, including shrubs. We recorded the approximate duration in years necessary for 10% and 50% woody cover. When multiple sites at a locality were described, we took minimum values.

We recorded associated environmental and compositional data from each study, including approximate geocoordinates of the site described, notes on substrate, field size and the typical composition of invaded herbaceous communities and initial woody colonists. Because some studies reported field



Figure 1 Years after abandonment until old fields are dominated by woody vegetation (measured as 50% woody cover) across the eastern USA, derived from 30 studies of old-field succession (Table 2).

size whereas others reported distances of study plots to field edges, we calculated a standardized measure of proximity to woody seed sources by transforming field-size estimates into edge distances by taking the half of the square root of field area. This measure is the maximum distance of a point in the centre of a field from the field boundary, assuming fields were approximately square.

We accessed climate data from DAYMET (<http://www.daymet.org>) to determine the average number of growing degree-days (GDD, annual mean, 1980–1997), which describes the accumulation of heat at a location and is a good indicator of both growing season duration and rates of biological activities such as plant growth. Too few studies reported detailed soil characteristics to allow a rigorous assessment of succession rate with respect to soil quality, but coarse-scale differences in soil properties between study locations can be estimated with standardized soil survey data. We used the ISRIC-WISE global grid of soil properties (Batjes, 2006), available at a 5 × 5 arc-minute resolution (c. 8 km) for the EDF, to estimate mean cation exchange capacity (CEC) for each study location. CEC measures the ability of soils to retain essential nutrients such as Ca, Mg and Fe, and is one widely available component of soil fertility. We also used an additional metric of site fertility related to agronomic productivity. Using the 1930 US Agricultural Census (US Department of Commerce, 1930), we recorded per-acre (0.405 ha) yields of corn (maize) for the counties of each of the sites in our study. These data represent soil conditions prior to the widespread use of industrial fertilizers after World War II; thus, per-acre corn yield serves as a phytometer

indicating the relative ability of nutrient-demanding herbaceous plants to grow across the latitudinal gradient. Corn yields in particular are a convenient measure of local soil fertility, in that corn is relatively insensitive to growing season length differences beyond its minimum seed maturity threshold (2–3 months, depending on genotype).

To analyse the latitudinal response of succession rates, we used ordinary least squares (OLS) regression with log-transformed variables of years to 10% and 50% woody cover. To address the possible influence of outliers on regression results, we compared OLS results with those obtained using robust regression, where fitting is performed by means of iterated re-weighted least squares, using the 'rlm' function in the MASS library for R (Venables & Ripley, 2002). We also calculated standardized residuals and Cook's distance for all values in both OLS regressions. In no case did robust regression results differ significantly from OLS regression results, nor did we detect any significant outliers based on Cook's distance (all less than 0.5). Only three values from the 10% cover regression were near the standardized residual outlier threshold of 2, and eliminating these values did not change the qualitative pattern. For these reasons we report results only from the OLS regressions. We analysed best-fitting multiple factor models for 10% and 50% woody cover variables using generalized linear models ('glm' in R 2.6.2) and evaluated competing models with corrected Akaike information criterion (AICc) tests (Burnham & Anderson, 2002). Competing models included all single- and multi-factor combinations of GDD, CEC and corn yield for each succession-rate variable.

RESULTS

Geographic variation in rates of succession

We found substantial variation in rates of succession at relatively small spatial scales. For example, two studies in the hills of southern Illinois (Voigt & Mohlenbrock, 1964; Bazzaz, 1968), with the same composition of herbaceous and woody dominants, documented woody dominance in 10 and 40 years, respectively. Two sites in southern Ohio, again having a similar composition of herbaceous and woody dominants, reached 50% woody cover in 25 years (Vankat, 1991) and 50 years (Barcus *et al.*, 1978).

At broader spatial scales, rates of woody species invasion into abandoned agricultural fields decreased with latitude, using both 10% and 50% woody cover estimates (Table 2, Figs 1 & 2). Latitude alone explained about a third of the variation in succession rates measured as years to 50% woody cover, and a quarter of the variation as years to 10% cover (Fig. 2a,b; both $P < 0.01$ in OLS regression; 50% rate variable $F = 11.79$ on 1,23 d.f., $R^2 = 0.34$; 10% rate variable $F = 8.57$ on 1,27 d.f., $R^2 = 0.24$). Succession rates were particularly fast in the south-eastern Piedmont (Fig. 1), where closed canopies could form in less than a decade after abandonment (McQuilken, 1940; Oosting, 1942; Keever, 1950; Nicholson & Monk, 1975). In contrast, in most old fields in the north,

woody colonization did not occur for more than a decade, and many were still dominated by herbaceous perennials several decades after abandonment, some for longer than 60 years (Thompson, 1943; Bard, 1952; Mellinger & McNaughton, 1975; Inouye *et al.*, 1987; Vankat, 1991).

Geographic patterns in old-field species pools

Our review revealed clear differences in the regional composition of old-field herbaceous dominants and woody pioneer species, which are supported by additional analyses of major Northeastern US (Gleason & Cronquist, 1991) and Southeastern US (Weakley, 2008) floras. The biggest contrast involves the dominant herbaceous perennials in northern and southern fields: in general, northern sites are dominated by rhizomatous Asteraceae (especially goldenrods, *Solidago* spp.) and rhizomatous grasses (especially *Poa pratensis* and *Agropyron repens*), whereas southern sites are dominated by bunchgrasses (especially broomsedge, *Andropogon virginicus*; little bluestem, *Schizachyrium scoparium*; and big bluestem, *Andropogon gerardii*) (Table 2). The bunchgrasses are commonly associated with more nutrient-poor soils, particularly on the south-eastern Piedmont, and are also common in the North on nutrient-poor or coarse-textured substrate (Bazzaz, 1963). Although *Solidago* species are widespread across the eastern USA, they rarely dominate old fields in the South, and those species that do have less capability for clonal growth than those common in the North (Radford *et al.*, 1964; Gleason & Cronquist, 1991; Weakley, 2008).

Several woody pioneer species are common across the EDF, including *Acer rubrum*, *Fraxinus americana*, *Juniperus virginiana* and *Prunus serotina* (Table 2). In the Northeast, important woody pioneers also include *Acer negundo* and *Pinus strobus*. Southern sites are typically dominated by yellow pines (*Pinus echinata*, *Pinus taeda* and *Pinus virginiana*), *Liriodendron tulipifera*, and, on wetter sites, *Liquidambar styraciflua* (Oosting, 1942). Closer to the western boundary of the EDF, *Diospyros virginiana*, *Sassafras albidum*, and *Celtis* and *Ulmus* species increase in prominence with *Juniperus*. Northern locations on sandy outwash include more northern pines (especially *Pinus rigida* and *Pinus banksiana*) as well as aspen (*Populus tremuloides*) and birches (*Betula* species).

Pioneer shrubs may be an important component of the north–south contrast in succession rates because they often play a large role in northern locations, especially as initial colonists that can both facilitate (Werner & Harbeck, 1982) and arrest (Putz & Canham, 1992) pioneer tree colonization. In contrast, pioneer shrubs are often absent from southern old fields, particularly where yellow pines predominate. In many Northeastern fields, gray dogwood (*Cornus racemosa*), sumacs (especially *Rhus typhina*) and hawthorns (*Crataegus* spp.) are common as natives, and an assortment of exotic species predominate in many locales, for example several species of honeysuckle (*Lonicera*) and buckthorn (*Rhamnus cathartica*). Sumacs such as *Rhus copallinum* and *Rhus glabra* are also important pioneers in the Midwest and parts of the interior

Table 2 Studies of old-field succession used to derive succession rates in the Eastern Deciduous Forest of North America, listed from high to low latitudes. See Table 1 for a definition of state codes.

Citation	State or province	10% woody cover	50% woody cover	Method	Latitude	Woody pioneers	Herb invaders	Max distance from seed source (m)
Inouye <i>et al.</i> , 1987	MN	40	60	Chronosequence	45.4	<i>Quercus rubra</i> , <i>Q. prinoides</i> , <i>Q. macrocarpa</i> , <i>Juniperus communis</i>	<i>Schizachyrium scoparium</i> , <i>Poa pratensis</i> , <i>Agropyron repens</i>	127
Howe, 1910	VT	20	ND	Anecdotal	44.5	<i>Pinus rigida</i> , <i>Betula papyrifera</i>	<i>Danthonia spicata</i> , <i>Solidago nemoralis</i>	NR
Thompson, 1943	WI	15	35	Chronosequence	43.8	<i>Pinus banksia</i> , <i>Populus grandidentata</i>	<i>Schizachyrium scoparium</i> , <i>Lespedeza capitata</i> and <i>Euphorbia corollata</i>	NR
Maycock & Guzikowa, 1984	ON	50	ND	Single site	43.3	<i>Rubus</i> spp.	<i>Agropyron repens</i> , <i>Poa pratensis</i> , <i>Solidago altissima</i>	116
Mellinger & McNaughton, 1975	NY	18	36	Chronosequence	42.9	<i>Cornus racemosa</i>	<i>Solidago altissima</i>	50
Evans & Dahl, 1955	MI	50	ND	Single site	42.5	<i>Quercus</i> spp., <i>Prunus serotina</i>	<i>Poa pratensis</i> , <i>Solidago (rigida and juncea)</i>	123
Beckwith, 1954	MI	5	25	Chronosequence	42.3	<i>Prunus serotina</i> , <i>Ulmus americana</i> , <i>Rhus</i> spp.	<i>Solidago</i> spp., <i>Poa pratensis</i>	71
Beckwith, 1954	MI	5	20	Chronosequence	42.3	<i>Rhus typhina</i> , <i>R. glabra</i> , <i>Cornus racemosa</i>	<i>Solidago</i> spp., <i>Aster</i> spp.	71
Lanyon, 1981	NY	6	12	Chronosequence	40.9	<i>Prunus serotina</i> , <i>Robinia pseudoacacia</i> , <i>Myrica pennsylvanicum</i>	<i>Solidago</i> and <i>Hieracium</i> (no species listed)	NR
Meiners <i>et al.</i> , 2002	NJ	10	25	Time series	40.5	<i>Juniperus virginiana</i> , <i>Acer rubrum</i> , <i>Rhus radicans</i>	<i>Solidago (juncea and graminifolia)</i> , <i>Hieracium florentium</i> , and <i>Poa pratensis</i>	47
Bard, 1952	NJ	10	60	Chronosequence	40.4	<i>Juniperus virginiana</i> , <i>Acer rubrum</i> , <i>Ulmus rubra</i>	<i>Solidago (nemoralis and graminifolia)</i> , <i>Andropogon (scoparius and virginicus)</i>	NR
Hanks, 1971	NJ	10	40	Chronosequence	40.1	<i>Acer rubrum</i> , <i>Liquidambar styraciflua</i>	<i>Solidago juncea</i> , <i>Andropogon virginicus</i>	NR
Keever, 1979	PA	5	20	Anecdotal	40.0	<i>Prunus serotina</i> , <i>Acer negundo</i> , <i>Ulmus rubra</i>	<i>Solidago nemoralis</i>	78
Levin, 1966	NJ	2	ND	Time series	39.7	<i>Rubus flagellaris</i> , <i>Quercus ilicifolia</i> , <i>Robinia pseudoacacia</i> , <i>Hudsonia ericoides</i>	<i>Digitaria sanguinalis</i> , <i>Conyza canadensis</i> , <i>Ambrosia artemisiifolia</i> , <i>Panicum</i> spp.	32
Vankat, 1991	OH	10	50	Chronosequence	39.5	<i>Fraxinus americana</i> , <i>Prunus serotina</i>	<i>Solidago canadensis</i> , <i>Festuca elatior</i>	74

Table 2 continued

Citation	State or province	10% woody cover	50% woody cover	Method	Latitude	Woody pioneers	Invaded herbs	Max distance from seed source (m)
Barcus <i>et al.</i> , 1978	OH	15	25	Time series	39.3	<i>Cornus florida</i> , <i>Sassafras albidum</i> , <i>Ulmus</i> , <i>Fraxinus</i> , <i>Prunus</i>	<i>Lespedeza</i> spp., <i>Solidago</i> spp., <i>Aster</i> spp.	61
Hopkins & Wilson, 1974	IN	10	ND	Chronosequence	39.3	<i>Acer negundo</i> , <i>Populus deltoides</i> , <i>Ulmus rubra</i> , <i>Juniperus virginiana</i> , <i>Prunus serotina</i>	<i>Solidago canadensis</i> , <i>Aster ericoides</i> , <i>Oenothera biennis</i>	123
Hoye <i>et al.</i> , 1979	OH	10	25	Chronosequence	39.1	<i>Acer negundo</i> , <i>Ulmus rubra</i> , <i>Fraxinus americana</i>	<i>Eupatorium rugosum</i> , <i>Geum virginianum</i> , <i>Phytolacca americana</i>	NR
Potzger & Potzger, 1950	IN	ND	15	Single site	39.1	<i>Juniperus virginiana</i> , <i>Liquidambar styraciflua</i> , <i>Acer rubrum</i>	<i>Andropogon virginicus</i>	60
Drew, 1942	MO	10	15	Chronosequence	38.7	<i>Diospyros virginiana</i> , <i>Sassafras albidum</i>	<i>Solidago nemoralis</i> , <i>Aster pilosus</i> , <i>Andropogon</i> spp.	NR
Hall, 1955	MO	10	30	Single site	38.5	<i>Diospyros virginiana</i> , <i>Quercus</i> spp.	<i>Andropogon</i> spp.	35
Bazzaz, 1968	IL	4	40	Chronosequence	37.3	<i>Diospyros virginiana</i> , <i>Sassafras albidum</i> , <i>Juniperus virginiana</i> , <i>Ulmus alata</i>	<i>Andropogon virginicus</i>	250
Voigt & Mohlenbrock, 1964	IL	7	10	Anecdotal	37.0	<i>Diospyros virginiana</i> , <i>Sassafras albidum</i> , <i>Juniperus virginiana</i>	<i>Andropogon virginicus</i>	NR
Keever, 1950	NC	5	10	Chronosequence	36.0	<i>Pinus taeda</i>	<i>Andropogon virginicus</i>	NR
Oosting, 1942	NC	5	8	Chrono+time series	36.0	<i>Pinus taeda</i> , <i>P. virginiana</i> , <i>P. echinata</i> , <i>L. styraciflua</i> (wet areas)	<i>Andropogon virginicus</i>	NR
Quarterman, 1957	TN	12	20	Chronosequence	35.5	<i>Celtis</i> , <i>Ulmus</i>	<i>Andropogon</i> spp.	NR
McQuilken, 1940	NC/SC/VA	5	8	Chronosequence	34.5	<i>Pinus taeda</i> , <i>P. virginiana</i> , <i>P. echinata</i>	<i>Andropogon virginicus</i> , <i>A. scoparius</i> , <i>A. tenarius</i>	200
Nicholson & Monk, 1975	GA	10	15	Chronosequence	33.5	<i>Diospyros virginiana</i> , <i>Prunus angustifolia</i> , <i>Pinus taeda</i> , <i>Pinus echinata</i>	<i>Andropogon scoparius</i>	71
Kurz, 1944	FL	5	15	Chronosequence	30.5	<i>Pinus echinata</i>	<i>Andropogon virginicus</i> , <i>Eupatorium</i> spp.	NR
Bonck & Penfound, 1945	LA	8	15	Chronosequence	30.1	<i>Morella cerifera</i>	<i>Solidago hirsutissima</i> (=S. <i>altissima</i>)	NR

NR, not reported.

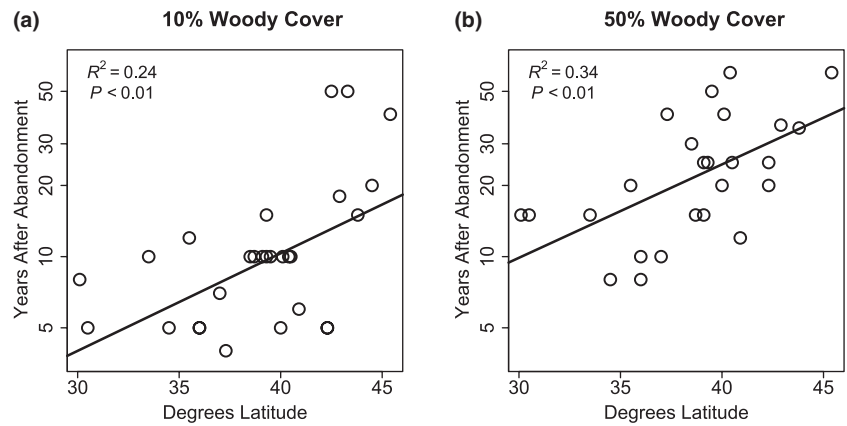


Figure 2 Rate of woody species colonization into old fields after abandonment across latitudes of the eastern USA, measured as years until (a) 10% and (b) 50% woody cover.

South, but, with minor exceptions on the coastal plain (e.g. *Prunus angustifolia*, *Crataegus* spp.), shrubs are not an important component of old-field succession in the South. *Rubus* species are also important in old fields across the eastern USA, particularly where persistent from previously established rhizomes.

Broad-scale predictors of succession rates

Bivariate relationships of the predictor variables relating climate, soils and field size to latitude and succession-rate variables are

presented in Fig. 3. Information on field size was available for 17 sites. There was no relationship between estimated field size and latitude ($P = 0.35$, $F = 0.90$ on 1,16 d.f.), and, consequently, no relationship between field size and either 10% cover ($P = 0.87$) or 50% cover ($P = 0.97$; Fig. 3). In all regions of the EDF, both wind- and animal-dispersed species play an important role (Table 1), with no systematic bias towards animal-dispersed species in the North and wind-dispersed species in the South. If anything, there is a greater dominance of animal-dispersed species in the Southeast and Mid-Atlantic. Thus, although dispersal can play an important role in determining rates of

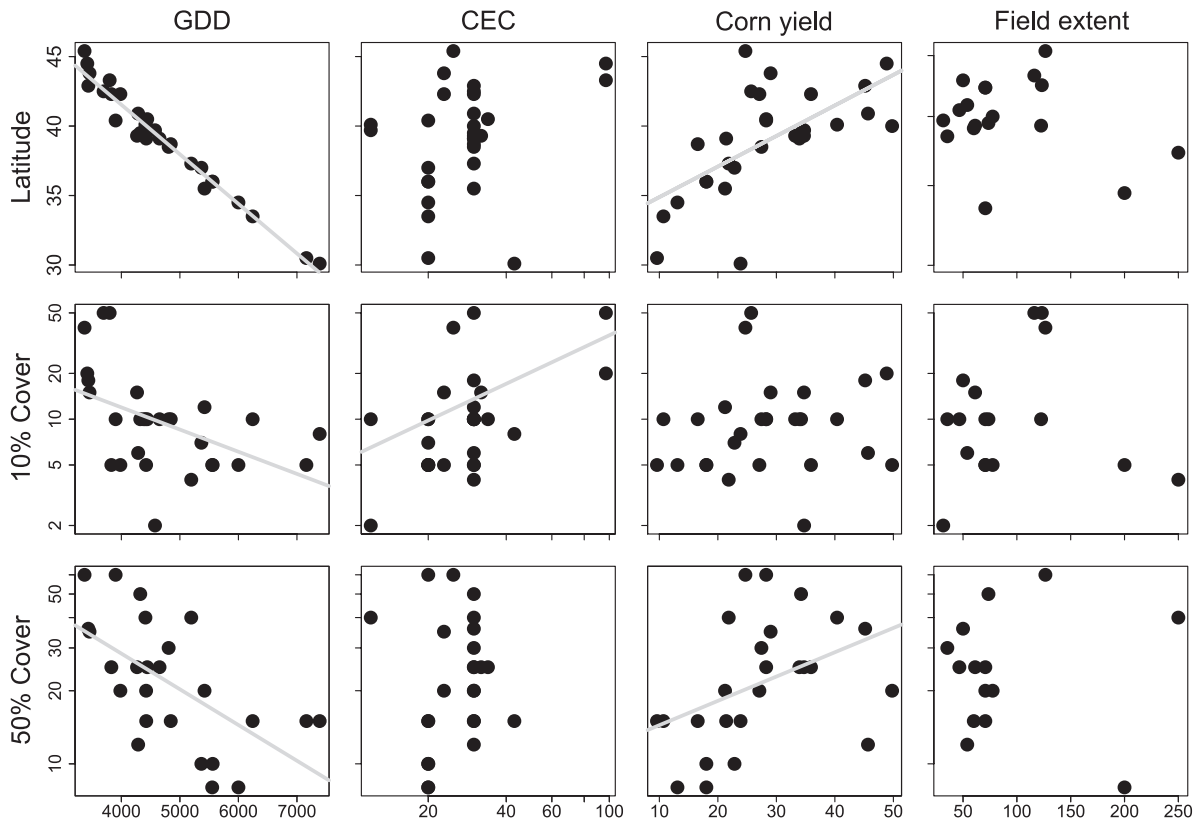


Figure 3 Bivariate relationships between dependent variables of latitude and rates of woody species colonization of old fields (years after abandonment until 10% and 50% woody cover) and predictor variables of growing degree-days (GDD), soil cation exchange capacity (CEC), corn (maize) yield in bushels per acre, and field extent (maximum distance to field edge, in metres). CEC and woody cover variables are log-transformed. Associated statistics are reported in the text; significant linear relationships in ordinary least squares regressions are indicated.

succession at local scales, it is unlikely to be the explanation for broad-scale variation in the rates of succession across the latitudinal gradient of the EDF.

Temperature regime and latitude are closely related for the 30 sites. Mean annual growing degree-days (GDD) is strongly correlated with latitude in our dataset ($r = -0.98$, Fig. 3), and thus similarly predictive of succession-rate patterns ($P < 0.01$ for both 10% and 50% cover variables in OLS regression; $F = 7.96$ and 13.57 on 1, 27 and 1, 23 d.f., respectively). Both soil-fertility indicators are also related to broad-scale succession rates (Fig. 3). Estimated CEC values for each study location are not related to latitude, but they are associated with years to 10% woody cover (Fig. 3; $F = 11.22$ on 1, 27 d.f., $P < 0.01$). Pre-agroindustrial corn yield from the county of each study is strongly related to latitude ($F = 18.42$ on 1, 27 d.f.; $P < 0.001$, $R^2 = 0.41$), and is predictive of succession rates in terms of years to 50% woody cover ($F = 4.88$ on 1, 23 d.f., $P < 0.05$).

Generalized linear models involving all predictor variables provided support for both climate and soil factors in controlling broad-scale succession rates, but varied by whether succession rates were measured as rates to woody establishment (10% cover) or dominance (50% cover). The best-fitting model for 10% cover included GDD, CEC and corn yield (Table 3), suggesting that climate and soil quality drive the rate of woody species establishment, and that corn yield indicates aspects of soil fertility beyond CEC. This three-factor model explained more than a third ($R^2 = 0.39$) of the variance in rate of woody establishment across the EDF. In contrast, GDD was the most significant predictor of number of years to 50% woody cover across sites in our dataset, and other factors were not supported after GDD was included (Table 3). Explained variance for the 50% cover variable was only half that for 10% cover ($R^2 = 0.21$).

DISCUSSION

We conclude from existing studies of old-field succession across the EDF that, although substantial variation in rates of

Table 3 Fitted parameter values with standard error (SE) and significance tests for best-fit generalized linear models predicting the number of years to 10% and 50% woody cover in old-field sites in the Eastern Deciduous Forest of North America, respectively.

Factor	Coefficient	SE	<i>t</i> -value
Years to 10% woody cover ($n = 28$)			
Intercept	4.68765	0.9459	4.96***
GDD	-0.00045	0.0001	-3.29**
CEC	0.01793	0.0079	2.26*
Corn yield	-0.03083	0.0142	-2.18*
Years to 50% woody cover ($n = 25$)			
Intercept	4.70200	0.4543	10.35***
GDD	-0.00034	0.0001	-3.68**

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

succession occurs at local scales, there is support for a latitudinal pattern of succession rates. Geographic differences in the composition and growth attributes of old-field herbaceous perennials and woody pioneer species may contribute to both the overall latitudinal pattern and regional variation in succession rates. We found support for the hypotheses that variation in climatic and edaphic factors may contribute to broad-scale variation in rate of succession.

Of the myriad abiotic and biotic factors that have been shown to be important drivers of succession rates in particular studies, we argue that three stand out as potential broad-scale drivers of succession, namely climate regime, soil fertility and the traits associated with different species pools of herbaceous and woody species. Given the limitations of our dataset, strong conclusions about the relative strengths of these mechanisms and whether the effects of climate and soil fertility are direct effects or indirect effects as mediated through changes in the species pool are premature. Furthermore, data are not available to test conclusively the hypothesis that latitudinal variations in colonization rates (e.g. distance to seed sources rather than field size) or herbivory drive the biogeographic patterns in rates of woody succession. Nevertheless, we find it striking that over a third of the variance in the rate of woody establishment can be explained by climatic and edaphic factors. These results suggest that attempts to understand what controls the rates of succession at different sites must take into account mechanisms operating at multiple spatial scales.

A hierarchical model of old-field succession rates across the EDF

Processes such as the dispersal limitation of woody colonists and their consumption by herbivores may often play an important role in the rate of old-field woody dominance at individual sites, but we suggest that these factors are more likely to vary on smaller spatial scales and thus act to add local variation to an underlying biogeographic pattern. For this reason, we posit a hierarchical model for processes influencing succession rates in old-field systems (Pickett *et al.*, 1987), focusing in particular on the intensity of competition between old-field herbaceous perennials and potential woody colonists (Fig. 4). This model incorporates well-supported mechanisms that vary at local scales (e.g. dispersal limitation, herbivory and site history) as well as the mechanisms developed here that are likely to vary at regional spatial scales. Our use of the term 'hierarchical' refers to a nested spatial hierarchy of factors regulating an ecological process, and does not necessarily imply a nested modelling structure. This model is intended as a working model, and its key assumptions and overall structure should be explicitly experimentally tested, ideally with an experimental design that includes controlled variation in climate, soil fertility and species pools across the extent of the EDF. For example, the establishment of identical herbaceous communities on a common soil substrate in fields across the EDF could establish the contribution of climatic variation to the biogeographic succession pattern.

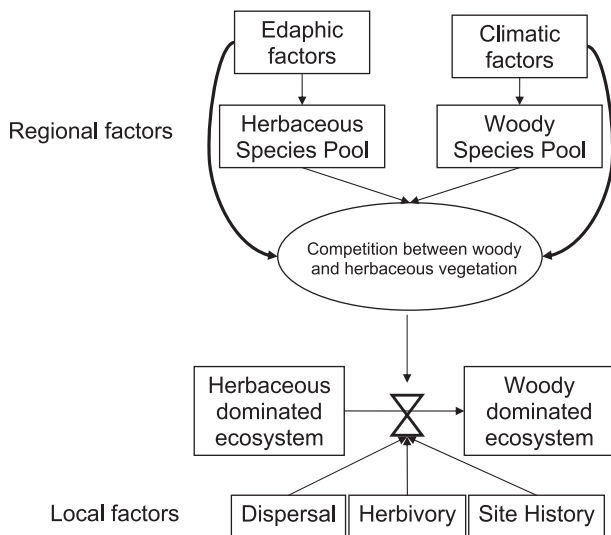


Figure 4 A hierarchical model of factors controlling rates of old-field succession across the Eastern Deciduous Forest of North America. See text for details.

We propose that processes acting at the regional scale control the extent to which resident herbaceous species are favoured in competition with woody seedlings, and that these processes depend on growth characteristics of the herbs (e.g. fast-growing clonal species versus stress-tolerant bunchgrasses) and woody species (e.g. slow-growing frost-tolerant species versus those of rapid apical dominance). The relative performance of herbaceous and woody species is also dependent on the fertility status of the soil and the climate regime. Because these factors tend to vary in concert from north to south across the EDF, it will be difficult to assess their relative importance without experimentation. Nonetheless, the threat of continued anthropogenic warming across the EDF suggests that additional study of the causation routes in Fig. 4 will be essential to predicting the extent to which successional processes will change over the next century.

Within particular EDF regions, we expect factors that vary locally, such as the intensity of woody seedling herbivory or the distance to the nearest propagule sources for potential woody colonists, to further affect woody seedling establishment. We further note that the environmental factors of temperature and soil nutrient regimes can also exhibit considerable variation at small scales (Fridley, 2009). In particular, an examination of differences in old-field succession rates across different topographic positions within the same landscape, which are likely to vary in temperature, moisture and nutrient regimes, may provide additional means to evaluate the importance of the routes of causation in Fig. 4.

An understanding of the factors that control the process of succession is critical for predicting the form and function of future ecosystems (Bazzaz, 1996). The USDA (2001) estimated that in the United States 42 hectares of farmland each hour are transformed to other uses, with half of this area reverting to open space or less intensive uses, and abandonment of

cropland is occurring at an increasing rate at a global scale (Cramer *et al.*, 2008). Our review presents a broad-scale pattern of how quickly these ecosystems will transition to forests that is not adequately explained by existing succession models. Despite more than a century of empirical study, there is still great potential for new insights into succession processes as this research moves into a more explicit global change framework.

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