Ecology, 100(2), 2019, e02579
© 2019 by the Ecological Society of America

The potential role of intrinsic processes in generating abrupt and quasi-synchronous tree declines during the Holocene

Tanjona Ramiadantsoa,[1,3] M. Allison Stegner,[1] John W. Williams,[2] and Anthony R. Ives[1]

[1]*Department of Integrative Biology, University of Wisconsin-Madison, Madison, WI 53706 USA*
[2]*Department of Geography and Center for Climatic Research, University of Wisconsin-Madison, Madison, WI 53706 USA*

Citation: Ramiadantsoa, T., M. A. Stegner, J. W. Williams, and A. R. Ives. 2019. The potential role of intrinsic processes in generating abrupt and quasi-synchronous tree declines during the Holocene. Ecology 100(2):e02579. 10.1002/ecy.2579

Abstract. Multiple abrupt and sometimes near-synchronous declines in tree populations have been detected in the temperate forests of eastern North America and Europe during the Holocene. Traditional approaches to understanding these declines focus on searching for climatic or other broad-scale extrinsic drivers. These approaches include multi-proxy studies that match reconstructed changes in tree abundance to reconstructed changes in precipitation or temperature. Although these correlative approaches are informative, they neglect the potential role of intrinsic processes, such as competition and dispersal, in shaping tree community dynamics. We developed a simple process-based community model that includes competition among tree species, density-dependent survival, and dispersal to investigate how these processes might generate abrupt changes in tree abundances even when extrinsic climatic factors do not themselves change abruptly. Specifically, a self-reinforcing (i.e., positive) feedback between abundance and survival can produce abrupt changes in tree abundance in the absence of long-term climatic changes. Furthermore, spatially correlated, short-term environmental variation and seed dispersal can increase the synchrony of abrupt changes. Using the well-studied, late-Holocene crash of *Tsuga canadensis* (eastern hemlock) populations as an empirical case study, we find that our model generates abrupt and quasi-synchronized crashes qualitatively similar to the observed hemlock patterns. Other tree taxa vary in the frequency and clustering of abrupt change and the proportion of increases and decreases. This complexity argues for caution in interpreting abrupt changes in species abundances as indicative of abrupt climatic changes. Nonetheless, some taxa show patterns that the model cannot produce: observed abrupt declines in hemlock abundance are more synchronized than abrupt increases, whereas the degree of synchronization is the same for abrupt decreases and increases in the model. Our results show that intrinsic processes can be significant contributing factors in abrupt tree population changes and highlight the diagnostic value of analyzing entire time series rather than single events when testing hypotheses about abrupt changes. Thus, intrinsic processes should be considered along with extrinsic drivers when seeking to explain rapid changes in community composition.

Key words: abrupt change; frequency dependence; hemlock decline; intrinsic processes; self-reinforcing feedback; spatial synchrony.

Introduction

Several mesic temperate tree species in eastern North America experienced one or more abrupt population declines during the warm interglacial climates of the Holocene, at spatial extents ranging from single sites to range-wide. These collapses are well documented by networks of fossil pollen records from lakes and mires, most of which have a pollen source radius on the order of 10^2 km and hence are well-suited for detecting landscape-scale changes in vegetation composition (Webb 1993). Well-known Holocene tree population collapses include declines in New England *Quercus* (oak) populations coincident with *Tsuga canadensis* (eastern hemlock) decline (Foster et al. 2006); *Fagus grandifolia* (American beech) decline during the last 3,000 yr (Booth et al. 2012*b*, Wang et al. 2016); early- to middle-Holocene conversions from forest to prairie at the prairie–forest ecotone in the upper Midwest (Umbanhowar et al. 2006, Williams et al. 2009); and a series of *Picea* (spruce) and *Pinus* (pine) declines across eastern North America at the Pleistocene–Holocene transition (Blois et al. 2011). Of these, perhaps the best documented is the collapse of *T. canadensis* ca. 5,700–5,000 calendar years before present (yr BP; Bennett and Fuller 2002, Booth et al. 2012*a*; B. Shuman, W. Oswald, and D. Foster, *unpublished manuscript*), which is notable both for the high magnitude of change and for

Manuscript received 28 November 2017; revised 13 June 2018; accepted 24 October 2018. Corresponding Editor: David Nogues Bravo.
[3] E-mail: ramiadantsoa@wisc.edu

the abruptness of the decline, spanning apparently <10 yr at some sites (Allison et al. 1986).

The decline of *T. canadensis* is particularly notable for its spatial extent (across the entire geographic range, roughly 1,500 km wide), and duration: *T. canadensis* abundances remained low at many locations for several thousand years. The decline was initially treated as a synchronous event (Bennett and Fuller 2002) but now appears to be quasi-synchronous, with most populations crashing between 5,500 and 5,250 yr ago in New England (Shuman et al. 2009), 5,000 yr ago in northern Michigan (Booth et al. 2012*a*), and as late as 3,800 yr ago at Spruce Pond, New York (Shuman et al. 2009). Such declines are important for understanding tree community responses to changing climate. They also represent well-documented case studies that speak more broadly to the general challenge of detecting and diagnosing the causes of abrupt change in ecological systems (Ratajczak et al. 2018).

Most explanations for these tree population declines invoke abiotic or biotic causes extrinsic to tree communities (Shuman 2012). Explanations for the *T. canadensis* decline include abrupt climate change (Foster et al. 2006, Booth et al. 2012*a*), pest outbreak (Davis 1981), or other more complex and not yet well understood mechanisms (Booth et al. 2012*a*). Efforts to attribute extrinsic causes have typically sought to match paleoecological records of tree decline to independent synchronous changes in one environmental driver. For example, the *T. canadensis* decline in New England has been linked to independent indicators of abrupt increased aridity in eastern North America (indicated by lowered lake levels) and nearby changes in Atlantic Ocean surface temperatures (Marsicek et al. 2013). Nonetheless, in some sites the declines in *T. canadensis* may have preceded the shift to drier conditions by roughly 200 yr (Booth et al. 2012*a*). Correlational matches among paleoecological and paleoclimatic proxies are important lines of evidence for extrinsic forcing but are not conclusive, and they do not exclude the influence of unobserved latent variables and intrinsic processes that are difficult to detect with proxy data.

Few studies have attempted to directly model the underlying ecological mechanisms and extrinsic and intrinsic processes that may have contributed to past abrupt ecological declines in Holocene tree populations. The potential role of intrinsic processes is particularly understudied. This gap sharply contrasts the literature on post-glacial range expansions, which has been the subject of numerous data syntheses and modeling studies, including pollen data syntheses, empirical species distribution models, community-level models, dynamic vegetation models, and customized models of biotic interactions among trees and pathogens (Moorcroft et al. 2006, Henne et al. 2011, Ordonez and Williams 2013, Saltré et al. 2013). For instance, theoretical work has explored potential mechanisms for the discrepancy between rapid northward expansion after glacier retreat and the measured dispersal ability of species (Reid's paradox; Kot et al. 1996, Clark 1998, Moorcroft et al. 2006). Dynamic vegetation models, widely used to study past and future forest dynamics during periods of environmental change, are a promising avenue for studying Holocene tree collapses, but they face the challenges of significant uncertainties and not-yet-reconciled disparities among observational and modeled time series of precipitation variability during the Holocene (Marlon et al. 2017). Given the rich literature modeling population dynamics in other systems that exhibit abrupt population collapses (Carpenter et al. 1999, Scheffer and Carpenter 2003, Mumby et al. 2007, Ives et al. 2008, Staver and Levin 2012), process-based community modeling approaches are promising, yet heretofore largely unexplored avenues for understanding the multiple factors contributing to mid-Holocene tree declines and community stability (Clark and McLachlan 2003).

In this work, we develop a modeling framework designed to explore the role of intrinsic processes and internal feedbacks in causing abrupt change in forest ecosystems. The general framework is based on the lottery model (Chesson and Warner 1981) in which tree species compete for limited space but have identical traits. We modify the classical lottery model to allow control of the following parameters: the strength of frequency-dependent survival, seed dispersal, and spatial autocorrelation in recruitment. We explore the role of these mechanisms in generating abrupt changes and in synchronizing those abrupt changes over large spatial areas. We compare modeled simulations to empirical patterns of Holocene tree dynamics from fossil pollen records drawn from the Neotoma Paleoecology Database[4] (Williams et al. 2018) using statistical approaches for detecting abrupt changes that are commonly used in the paleoecological literature. In comparing models to data, our goal is not to test whether the models fit the data and from this infer the processes underlying the observed abrupt changes in tree abundance. Instead, our goal is to ask whether the intrinsic processes in the models could potentially generate abrupt changes similar to the data, even though the model contains neither abrupt nor long-term changes in the environment. If the models show that intrinsic processes could generate abrupt changes, then hypotheses explaining observed abrupt changes in tree abundance should be expanded to include both extrinsic and intrinsic processes (Williams et al. 2011, Seddon et al. 2014).

Methods

Model description

Our model is based on the lottery model (Chesson and Warner 1981, Chesson 1985, 2000) and simulates the changes in frequency of N species through time and across space. The model is designed to describe species, like trees, that compete for space in the landscape, where a given location can be occupied by only a single individual.

[4] www.neotomadb.org

Competition thus occurs at the establishment stage, after a space is vacated by the death of the last occupant.

The model assumes three levels of spatial hierarchy. The regional level (e.g., eastern North America, in the case of *T. canadensis*) is spatially explicit and consists of an $X \times Y$ grid of sites. Sites are square cells that, here, are on the order of 10^1 to 10^2 km across, roughly matching the ecological source area represented by pollen records obtained from lakes and mires sediments that are the primary empirical data for Holocene tree decline (Webb 1993, Sugita 2007, Dawson et al. 2016). The site level encompasses a collection of locations (microsite level) that can only be occupied by a single individual. We assume that the number of locations within a site is large and spatially implicit. Therefore, we track species densities as the proportion of microsites occupied by each species within a site. We assume that there are no unoccupied sites, so species proportions sum to one, an assumption that is reasonable for the closed-canopy structure typical of eastern deciduous forests. The relative abundance of species i within a site is denoted by $p_{i,x,y}(t)$, which represents the proportion of locations occupied at a site with coordinate (x, y) at time t. For ease of notation, we omit the indices x and y unless they are required for clarity. We assume that the environment is homogenous within a site and that the seeds produced by individuals are spread uniformly throughout a site. Forest dynamics within a site are driven by the death of individuals occupying locations and their replacement by individuals of the same or different species. An individual of species i has a survival probability of u_i, so at each time step, locations are vacated due to the death of residents with probability $(1 - u_i)$. Thus, for a community with N species within a site, the proportion of locations that are available for colonization in time step t is

$$\left(1 - \sum_{j=1,\ldots,N} p_j(t)u_j\right)$$

where the second term is the sum of all species from 1 to N. Each empty location is colonized by one individual, and the success of a species colonizing a location is assumed to be proportional to the species' contribution to the total seed pool for the site. We denote this as b_i, the site-level per capita recruitment rate of species i. (This is not a frequency-dependent process, because increasing abundance [or frequency] does not increase the per capita recruitment.) Recruitment is the product of fecundity, seed survival, and establishment. The probability that an empty location is colonized by species i is

$$\frac{p_i(t)b_i}{\sum_{j=1,\ldots,N} p_j(t)b_j}.$$

Combining survival and colonization, the proportion of locations occupied by species i at time $t + 1$ is

$$p_i(t+1) = p_i(t)u_i + \left(1 - \sum_{j=1,\ldots,N} p_j(t)u_j\right)\frac{p_i(t)b_i}{\sum_{j=1,\ldots,N} p_j(t)b_j}. \quad (1)$$

This equation does not account for age structure in the tree population, but instead assumes that seedlings become reproductive trees in a single time step, representing one decade in the model. This simplifying assumption is appropriate for application of the model to forest dynamics across the Holocene. The site-level per capita recruitment rate is stochastic, and we assume that b_i follows the lognormal distribution

$$b_i \sim e^{\log(\beta_i)+\varepsilon_i}$$

where $\varepsilon_i \sim N(0, \sigma^2)$ follows a normal distribution with mean 0 and variance σ^2 that is independent among species, and β_i is the per capita recruitment (seed production and seedling survival and establishment) for species i when σ^2 is zero.

To generate spatial autocorrelation in the environmental variation affecting tree dynamics among sites, we decompose the variance in recruitment into a within-site (local) component σ_l^2 and an among-site (global) component σ_g^2 so that

$$\sigma^2 = (1 - \rho)^2\sigma_l^2 + \rho^2\sigma_g^2 \quad (2)$$

where ρ is the strength of spatial autocorrelation. When $\rho = 0$, recruitment for a species is independent among sites, while when $\rho = 1$, recruitment for a species is identical among all sites within the region. Thus, ρ governs the degree of regional synchrony of recruitment for a given species. Note that variation in recruitment is not autocorrelated through time because values of b_i are independent from one time step to the next. Therefore, the variation in recruitment is not subject to intermediate or long-term trends in the environment. Because this recruitment term effectively includes juvenile survival for up to 10 yr, modeling recruitment as a function of regional environmental variation can be thought to reflect the narrower environmental tolerance of juveniles in many tree species (Jackson et al. 2009).

Spatial synchrony among sites can be generated not only through regional autocorrelation in environmental fluctuations ($\rho > 0$), but also through propagule dispersal. Therefore, we modified the original lottery model to include dispersal among sites (Clark and McLachlan 2003, Blaauw et al. 2010, Usinowicz 2015). We assume a fraction f of seeds within a site disperses evenly across the eight neighboring sites, while a proportion $(1 - f)$ remains in the source site. For simplicity, we assume that seed survival and establishment rates are constant. Therefore, the total recruitment rate of species i at location (x, y) due to dispersal is

$$B_{i,x,y}(t) = (1-f)p_{i,x,y}(t)b_{i,x,y}(t) + \frac{1}{8}f \sum_{\substack{m,n=-1 \\ (m,n)\neq(0,0)}}^{1} p_{i,x+m,y+n}(t)b_{i,x+m,y+n}(t). \quad (3)$$

Dispersal is incorporated into Eq. 1 by replacing $p_{i,x,y}(t)b_i$ with $B_{i,x,y}(t)$.

We also modified the lottery model to include frequency-dependent effects, in which survival depends on the frequency of species $p_i(t)$ within sites. We assume that the survival probability u_i follows a logistic function

$$u_i(t) = \frac{\nu_i}{\nu_i + (1-\nu_i)e^{-sp_i(t)}} \quad (4)$$

where s measures the strength of frequency-dependent survival, and v_i is the survival when there is no frequency dependence ($s = 0$). A positive value of s means survival increases as the frequency of the species increases. The functional form of $u_i(t)$ is the same for all species.

Model implementation and parameter values

Although the model is designed as a general framework for investigating the effect of community processes on abrupt changes in species abundance, for ease of interpretation we parameterized the model with spatial and temporal scales comparable to those of the empirical data. We simulated a region of $32 \times 16 = 512$ grid cells where one cell is about 50×50 km. One time step in the simulation was equivalent to one decade, and the simulation was run for 11,700 yr. To summarize the simulated data for comparison with the empirical data, we subsampled the 512 grid cells by selecting 32 sites that are equally spaced along the rows and the columns. The empirical records of *T. canadensis* relative abundances (henceforth referred to simply as abundances) over the Holocene typically have on the order of 100 data points, so to mirror these data we subsampled the modeled time series every 10 time steps (i.e., 100 yr).

To investigate the role of the strength of self-reinforcing feedback in survival (s in Eq. 4), dispersal (f in Eq. 3), and regional autocorrelation (ρ in Eq. 2) in the abruptness and quasi-synchrony of population changes, we systematically varied each parameter while keeping the others fixed. To separate the effect of dispersal from regional stochasticity in generating synchrony, we kept $\rho = 0$ while varying f from 0 to 0.5. Conversely, we kept $f = 0$ while varying ρ from 0 to 0.8. As ρ varied, we held σ constant by maintaining the same value for the local component σ_l and adjusting the global component σ_g for each value of ρ. For each combination of parameters, we ran 100 replicates and computed the average.

We assumed that the modeled community consists of $N = 3$ species with baseline survival $\nu = 0.8$ and recruitment $\beta = 20$. To mimic the low initial abundance of *T. canadensis* and other thermophilous tree taxa at the start of the Holocene, we set the initial frequency of the first species representing *T. canadensis* to 2%, and the second and third species to 49% each.

Empirical comparison with fossil pollen data

We conducted two sets of analyses using empirical fossil pollen data sets from the U.S. Midwest and eastern North America. In the first, we assessed the number and temporal clustering of abrupt change in six deciduous (*Alnus*, *Fagus*, *Juglans*, *Platanus*, *Tilia*, and *Ulmus*) and four coniferous (*Picea*, *Pinus* subgenus *Pinus*, *Pinus* subgenus *Strobus*, and *Tsuga*) tree taxa that are common in Holocene fossil pollen records in eastern North America. We only searched for signals of abrupt change in sites with clear palynological evidence that the parent plant taxon was present near the site. We assume a taxon is present at a site when its relative abundance exceeds the taxon-specific "var05" threshold as in Nieto-Lugilde et al. (2015). In the second analysis, we focused on *T. canadensis*, which showed the greatest number of abrupt changes, and compared empirical patterns of abundance and abrupt change to simulations, in order to explore whether the model produces patterns of abrupt change that qualitatively resemble observations. For this analysis, we used 10% as the relative abundance threshold for selecting fossil pollen sites for abrupt change analysis, which is a higher threshold intended to select sites in which *T. canadensis* was not just "present" but common.

Site selection

We obtained pollen data from lake core and peat records from the Neotoma Paleoecology Database (see footnote [4]) using the "neotoma" package in R (Goring et al. 2015). We selected sites from across the upper Midwest and eastern United States (within longitude $-60°$ to $-105°$, and latitude 25° to 55°). Pollen was grouped at the genus level for all taxa, expect for *Pinus*, which was grouped at the subgenus level: *Pinus* subgenus *Pinus* and *Pinus* subgenus *Strobus* (see Appendix S1 for more details). *T. canadensis* is the only species in the genus *Tsuga* present in our study region, and so we assume that all pollen identified as *Tsuga* in the sites we analyzed belongs to *T. canadensis*.

In the multi-taxon analyses, we focus on samples from 8,000 to 1,000 yr BP to remove the effects of deglaciation and major anthropogenic impacts. This contrasts with our analyses specific to *Tsuga*, where we included samples from 11,700 to 1,000 yr BP. We restricted our analysis to sites with adequate pollen sampling resolution and age control by including only sites (1) with at least 20 pollen samples, (2) with an average pollen sampling interval ≤200 yr, and (3) which had a ratio of total record duration to number of chronological controls that was ≤2,000 yr. Biostratigraphic chronological controls that were older than 500 yr BP were excluded from

our tally. Five sites: Sharkey Lake, Tower Lake, Jones Lake, Chesapeake Bay, and Fox Lake had isolated instances of multiple samples at the same depth, which we averaged after calculating pollen proportions at those depths. Our search criteria produced 70 high-resolution sites (Appendix S1: Table S1).

Age-model reconstruction

Thirty sites had existing calibrated radiocarbon age-depth models in the Neotoma Database (Appendix S1: Table S1). For all other sites, we built age-depth models using the "Bchron" package in R (Parnell 2016), which fits a nonparametric age model using the compound Poisson-gamma model of Haslett and Parnell (2008). To create the chronologies, we used the age control data stored in Neotoma, but only included age controls that were radiocarbon dates, pollen biostratigraphic controls that were <500 yr old (i.e., indicators of EuroAmerican settlement), and the age of the core top (i.e., the year when the core was collected). For core top dates that lacked age error estimates, we designated error as 10± years to approximate the amount of time averaging at the top of a lake sediment core (Goring et al. 2012). We used the IntCal13 Northern Hemisphere curve to calibrate radiocarbon dates (Reimer et al. 2013). Newly generated age-depth models were visually inspected to ensure that the model fit the chronology controls reasonably well.

Detecting abrupt changes and quantifying synchrony

To identify abrupt changes in modeled and empirical percent abundance data, we used Bayesian change point analysis (BCP) implemented in the "bcp" package in R (Erdman and Emerson 2007, 2008, Wang and Emerson 2015). Bayesian change point analysis fits a piecewise linear function and then calculates the posterior probability of abrupt change at each point in the time series. We assume an abrupt change occurred when the probability is larger than 0.5. We found that the threshold probability of 0.5 identifies the abrupt changes that are often qualitatively identified in studies of the *Tsuga* decline (Results and Appendix S2: Fig. S1). For the MCMC sampling, we used 10,000 iterations after an initial burn-in of 1,000. We set $w0 = 0.2$ (the default recommended by Barry and Hartigan 1993), where $w0$ is the parameter in the uniform prior on the signal-to-noise ratio, and we used $p0 = 0$, where $p0$ is the prior value on change point probabilities, in order to minimize the sensitivity of the model to short-term outliers.

To summarize the degree of synchrony of abrupt changes across the modeled region, we used the coefficient of variation (CV) of the waiting time between successive abrupt changes. We separated and sorted the abrupt increases and decreases detected across all sites in the region, calculated the duration between successive abrupt changes, and computed their respective CVs. A low CV indicates no temporal patterns of aggregation (lack of synchrony among sites), whereas a high CV implies temporal clustering of abrupt changes.

When using CV as an index of synchrony in the model simulations, a potential artifact is introduced by the use of identical time steps for all simulations. If uncorrected, this effect will artificially inflate the CV of timing of abrupt change events, because abrupt changes at two sites that occur within a 100-yr window would be recorded as occurring at the same time. To remove the inflation of the CV caused by sampling time series simultaneously, we added uncertainty in our sampling by adding a random number with uniform probability between −50 and 50 yr of the time step, thereby blurring the distribution of times within each 100-yr time step.

The simulation code was written in Mathematica (Wolfram Research 2017), while *T. canadensis* data extraction and analysis were conducted in R (R Core Team 2016). Code is available in the Github repository (see Data Availability).

Results

Abruptness of changes

Although the community model contained no differences among species or among sites and no extrinsic forcing, simulated time series showed patterns of abrupt increases and decreases, identified by BCP, that resembled patterns in the fossil pollen record (Fig. 1). In the fossil pollen data, the number and ratio of abrupt increases and abrupt decreases varied widely among taxa (Fig. 2d). From 8,000 to 1,000 yr BP, abrupt changes were most common for *Tsuga*, *Ulmus*, *Fagus*, and *Picea*. There were as many abrupt increases as decreases for *Tsuga*, *Picea*, *Pinus* subgenus *Pinus*, and *Pinus* subgenus *Strobus*. In contrast, *Fagus* underwent more abrupt increases than decreases, whereas *Ulmus* showed the opposite pattern. We view these as largely driven by initial conditions, given that *Fagus* expansion at many sites began after 8,000 yr BP, while *Ulmus* abundances were initially high at many sites in the western part of the domain in the early Holocene.

Our model showed that the likelihood, magnitude, and synchrony of abrupt changes were sensitive to model parameter settings. Increasing the strength of self-reinforcing feedback in survival, s (Eq. 4), amplified the magnitude of abrupt changes (Fig. 2, left column). When s was zero, the time series resembled a random walk, and BCP did not detect abrupt changes (Fig. 2a). For intermediate values of s (e.g., 0.25), abrupt changes began to emerge (Fig. 2b), and for high values of s (e.g., 0.4), abrupt changes became clearly detectable (Fig. 2c).

The strength of frequency dependence also increased the number of abrupt changes detected in the time series (Fig. 2e, f). Abrupt increases and decreases were equally likely when all species began at the same frequency (Fig. 2e). However, when the focal species started at a

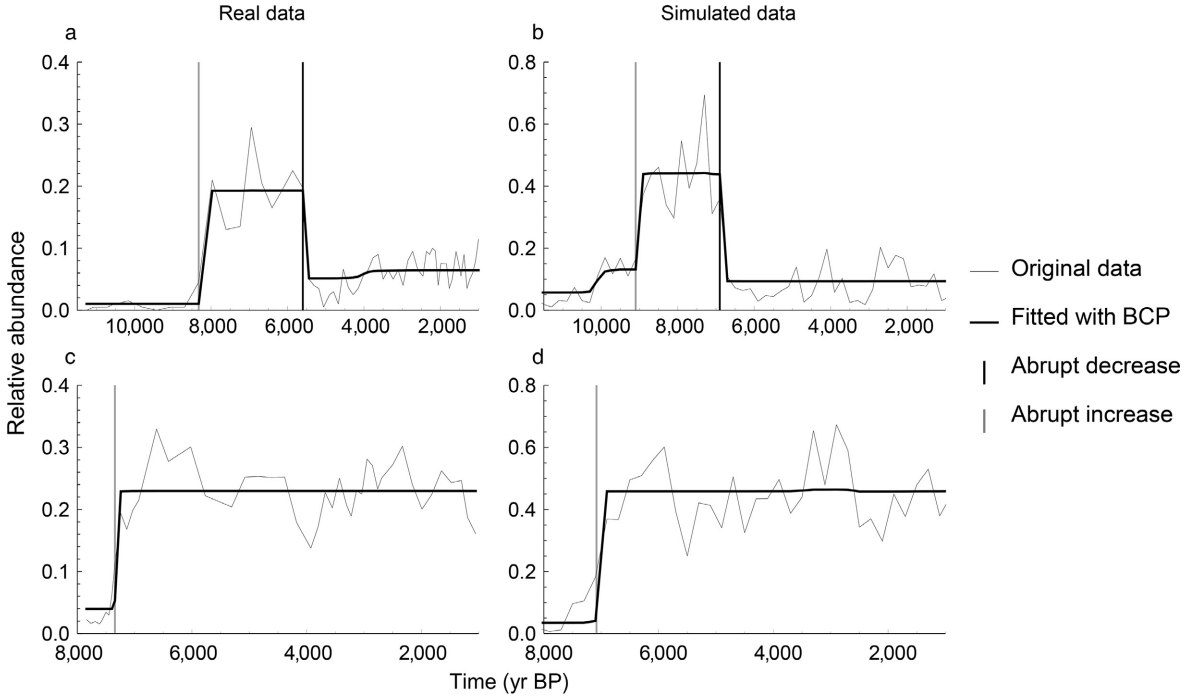

FIG. 1. Examples of time series fitted with Bayesian change point analysis (BCP). Panels a and c show the relative abundances of *Tsuga* (Cranberry Lake, Neotoma data set ID 516, 44.1° N, 78.1° W) and *Fagus* (Hams Lake, Neotoma data set ID 1002, 43.2° N, 80.4° W). Panels b and d show simulated time series from the lottery model for purposes of comparison. To mimic the empirical data, the time points were sampled every 200 yr. Thin and thick black lines represent original and BCP-fitted time series. The black and gray vertical lines represent abrupt decrease and increase, respectively. BP, before present. Parameters for the simulated data: strength of frequency-dependent survival $s = 0.4$, standard deviation of environmental variation σ = standard deviation of within-site (local) component of environmental variation $\sigma_l = 0.8$, fraction of seeds dispersed across the eight neighboring sites $f = 0$, strength of spatial autocorrelation $\rho = 0$.

low initial frequency, abrupt increases tended to occur more often than abrupt decreases (Fig. 2f), which is consistent with the empirical asymmetry in the ratio of abrupt increases to decreases in *Fagus*. In summary, increasing the strength of self-reinforcing feedbacks between abundance and survival increased the likelihood that abrupt changes would occur, and increased the magnitude when they did.

Distribution of abrupt changes across all taxa

Abrupt changes were observed across our spatial and temporal domain (Fig. 3). In total, there were as many abrupt increases as decreases. There were no conspicuous sub-region where abrupt changes were either common or absent. In fact, sites with abrupt changes were geographically near sites where no abrupt changes took place (Fig. 3a, c). Overall, around one-half of the sites had no abrupt changes. The clustering of abrupt increases and decreases also varied widely (Fig. 3b, d). Abrupt decreases appeared to be more synchronous than abrupt increases (Fig. 3b, d). Individual taxa showed signals of clustered abrupt change (e.g., *Tsuga*, *Ulmus*, and *Fagus* increases, *Picea* decreases), based on the CV metric (Appendix S1: Fig. S1). Other taxa showed no signs of temporal clustering (*Pinus*), or few signs of abrupt change (*Tilia*, *Platanus*, *Alnus*). Additional details for taxon-specific analyses are reported in Appendix S1.

Simulated and observed synchrony: T. canadensis

Twenty-seven high-resolution and well-dated fossil pollen data sets record an abrupt change in *T. canadensis* between 11,700 and 1,000 yr BP. As previously reported, a key feature of the abrupt changes in *T. canadensis* during the Holocene is the quasi-synchrony of the declines (Shuman et al. 2009, Booth et al. 2012*a*; B. Shuman, W. Oswald, and D. Foster, *unpublished manuscript*). Our BCP analyses confirmed that most abrupt declines clustered between 6,000 and 3,500 yr BP, although a few declines were also detected outside that window (Figs. 4a, 5a, c). However, for 11,700–1,000 yr BP, abrupt increases were more common than decreases in the empirical data; we detected roughly 74% more abrupt increases than decreases in *T. canadensis* across all time series. This is consistent with our simulations, where abrupt increases were more common than decreases (up to 68%) if the focal species started at low frequency (Figs. 2f, 4b, d). The CV

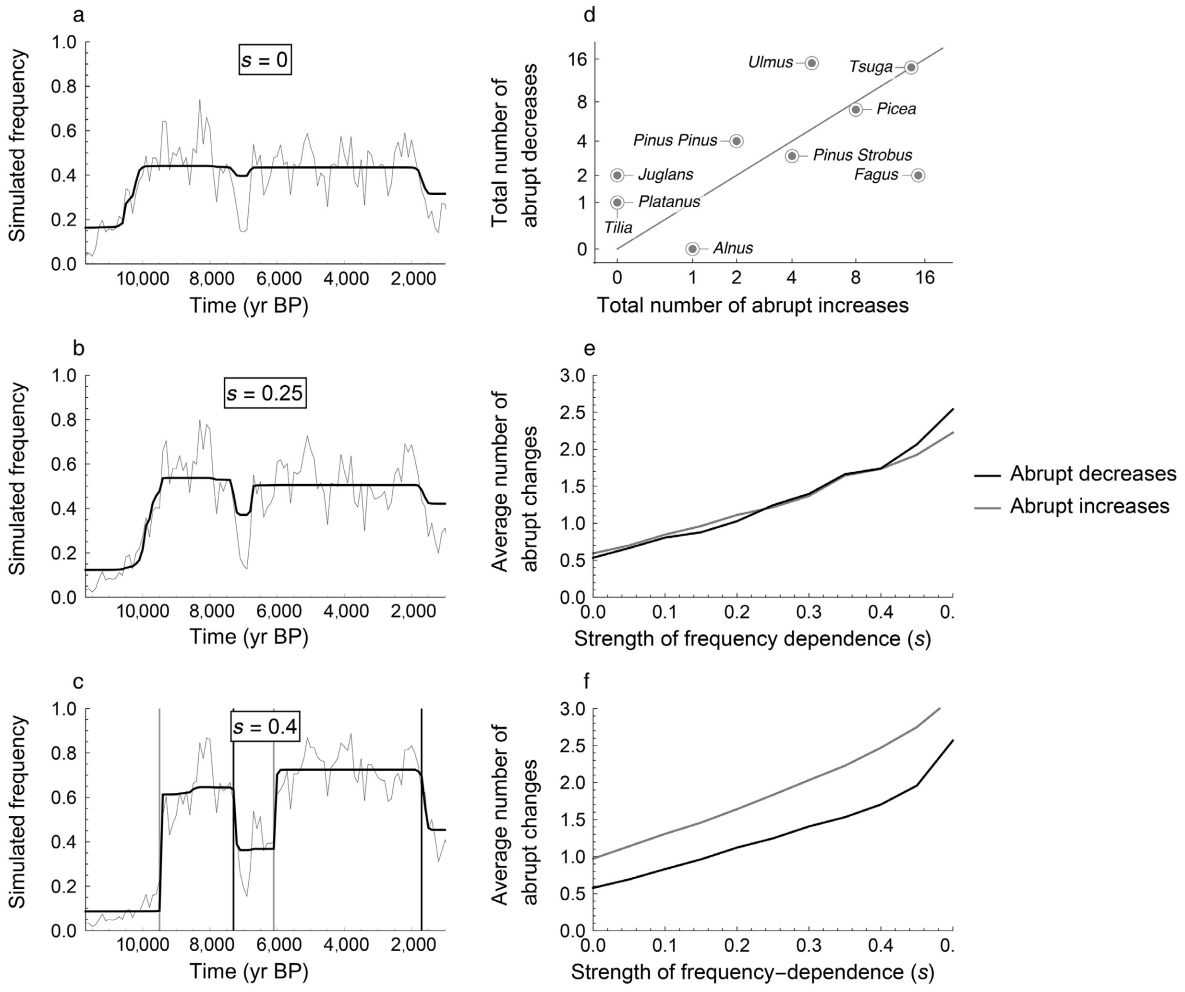

FIG. 2. The probability of abrupt changes increases with the strength of frequency dependence. Panels a–c show three examples of time series in which the strength of density dependence increases while all other parameters are kept constant. The vertical lines show the occurrences of abrupt increases (gray) and abrupt decreases (black). Panel d shows the number of abrupt decreases vs. abrupt increases (identified by Bayesian change point analysis) for all taxa between 8,000 and 1,000 yr BP on a logarithmic scale. The thin gray line gives the one-to-one line. Panels e and f show the increase in the average number of abrupt decreases (black) and increases (gray) per site as the strength of frequency dependence increases, with panel e giving the case of equal and panel f giving the case of low initial frequency for the focal taxon. Parameters: $\sigma = \sigma_1 = 0.8$, $f = 0$, $\rho = 0$.

(measuring synchrony) was much higher for abrupt decreases (CV = 2.42) than for abrupt increases (CV = 1.3) in the empirical data (Fig. 5c, e).

In the model, quasi-synchronous crashes were created by regional autocorrelation in recruitment. In an example simulation (Fig. 5b, d), around 6,000 yr BP all populations crashed nearly synchronously. Low abundances then persisted for about a 1,000 yr before recovering, and even after the recovery abundances were generally lower than prior to the crash (Fig. 5b), a pattern similar to observations (Fig. 5a). In contrast to the empirical data, however, this model also generated quasi-synchronized abrupt increases (Fig. 5e, f).

Using simulations with no environmental autocorrelation ($\rho = 0$), abrupt changes were not synchronized, as shown by the low CV ≈ 1; this is similar to the CV for abrupt increases of *T. canadensis* in the pollen records (Fig. 5e). However, increasing ρ increased the CV of both abrupt increases and abrupt decreases (Fig. 6a). These results illustrate that regional autocorrelation in recruitment rates can generate quasi-synchronized abrupt declines similar to those seen in the *T. canadensis* pollen data yet also generates quasi-synchronized abrupt increases that are not seen in the data.

In the model, synchrony of abrupt changes also increased with dispersal (Fig. 6b). However, the increase in CV due to environmental spatial autocorrelation (Fig. 6a) was linear and had a steeper slope than did the increase in CV produced by increased seed dispersal (Fig. 6b), thus indicating that environmental spatial autocorrelation is the more potent source of synchronized abrupt changes. Dispersal induced little synchrony (low

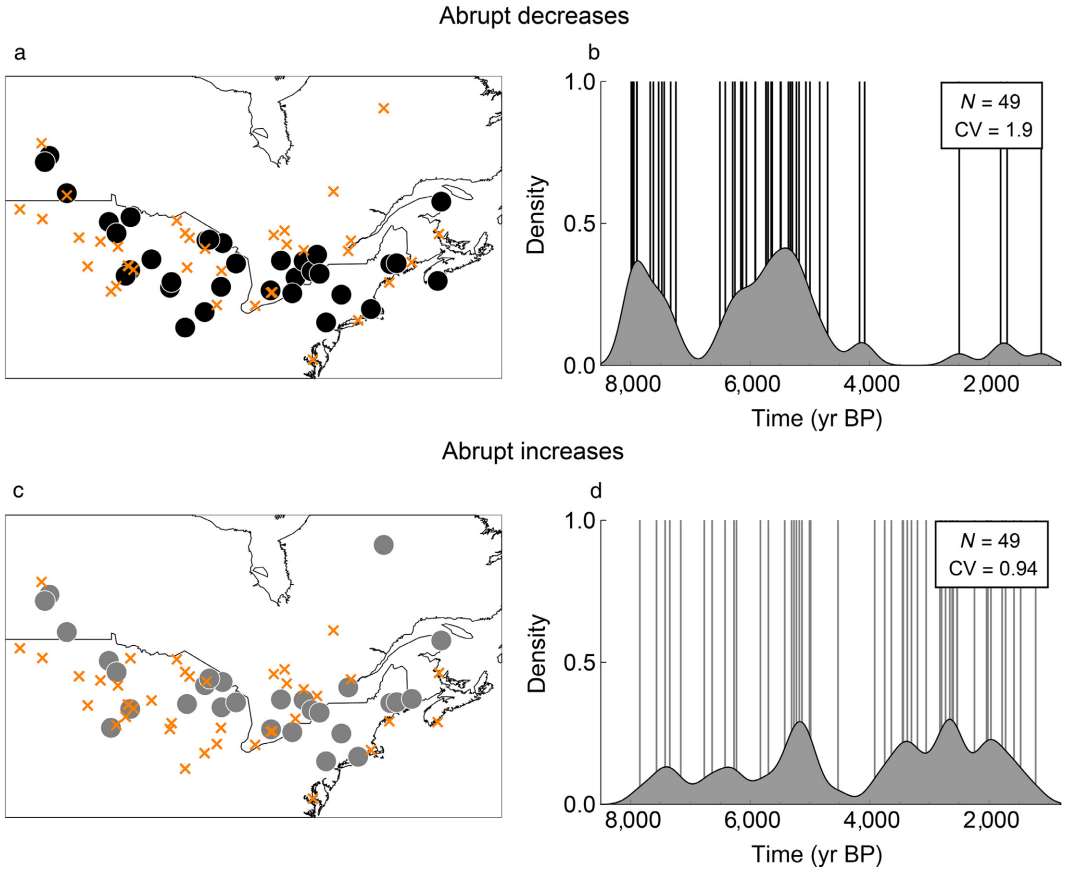

FIG. 3. Spatial and temporal distribution of abrupt decreases (top) and increases (bottom) for all taxa between 8,000 and 1,000 yr BP. Panels a and c show sites where abrupt changes occurred (circles) and sites where no abrupt changes were detected (orange cross). Panels b and d show the timing of all abrupt changes. The smooth histograms represent the density of abrupt changes through time. The total number of abrupt changes is denoted by *N*. Coefficient of variation (CV) measures synchrony.

CV) unless a significant proportion of the seeds (above 40%) are dispersed outside the source cell. In fact, to match the synchrony of the abrupt decline in the empirical data set (CV = 2.4, Fig. 4c) requires that more than 50% of the seeds be dispersed outside the source cell (Fig. 6b). Because the scale of cells in our simulations are set to roughly 50 × 50 km to match the pollen data, this is an unrealistically high dispersal distance for *T. canadensis*.

Discussion

During the Holocene, several tree species underwent abrupt and quasi-synchronous declines that are often attributed to broad-scale changes in climate or other extrinsic variables (Booth et al. 2012*b*, Shuman 2012, Marsicek et al. 2013, Wang et al. 2016, but see Blaauw et al. 2010). Here, we used a variant of the lottery model to show that intrinsic processes within communities can generate similar patterns of abrupt decline without requiring any long-term and persistent changes in the environment, such as multi-centennial droughts. In our model, abrupt decline is a manifestation of the system shifting from one stable community composition to another. These multiple stable communities are created by frequency-dependent survival, which generates a self-reinforcing feedback process (Holling 1973, May 1977). Spatial synchrony in abrupt changes can emerge from spatial autocorrelation in seedling recruitment or from seed dispersal (Ranta et al. 1999, Walter et al. 2017). Here, the modest effects of seed dispersal on synchronization (Fig. 6) suggests that this mechanism is not the major agent of synchronization at the region-wide scales considered here.

Environmental variability is intentionally not included as a deterministic driving variable in our model and so all abrupt changes and persistent community states emerge as a result of intrinsic, community-level processes, without any sustained or persistent environmental forcing. Environmental variability is instead treated here as a stochastic, white-noise process, with both site-level and regional variation, the strength of the latter being determined by the autocorrelation term (ρ, Eq. 2). By treating environmental variability as a white-noise process, we show how persistent environmental forcing (e.g., multi-centennial droughts or persistent periods of aridity) is not necessary

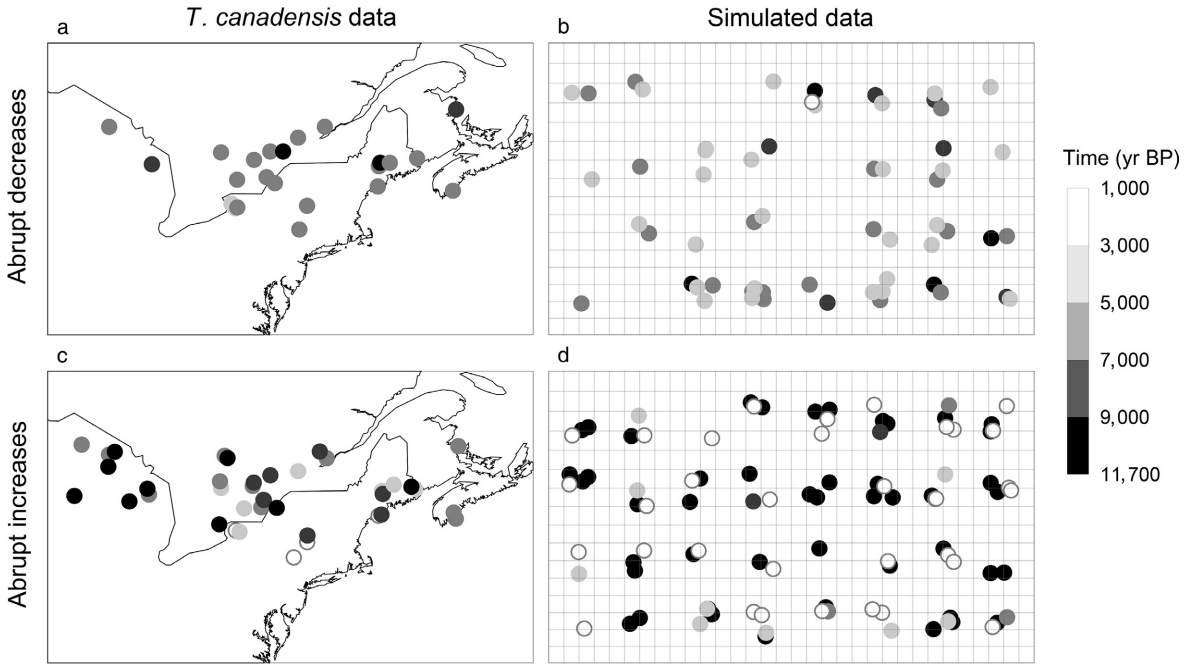

FIG. 4. Spatial and temporal distribution of (a, b) abrupt decreases and (c, d) increases (bottom) for *Tsuga* in northeastern United States and southern Canada (left) from 11,700 to 1,000 yr BP and an example of simulated data (right). Overlapping dots are slightly displaced for clarity. The hemlock data are based on fossil pollen data drawn from the Neotoma Paleoecology Database (see footnote [1]; Appendix S2: Table S1). The simulated data are based on 32 equally spaced "sites" (grid cells); each cell is about 50 × 50 km. Parameters: $s = 0.3$, $\sigma = \sigma_1 = 0.7$, $f = 0$, $\rho = 0.5$. yr BP, years before present.

to generate persistent declines of *T. canadensis*. Abrupt and synchronized changes in ecological communities, past or present, can be caused by the interaction between intrinsic ecosystem processes that generate frequency-dependent dynamics and additional processes that generate temporal clustering of abrupt changes such as spatially autocorrelated environmental variation and dispersal.

In our model, abrupt changes are caused by frequency-dependent survival: when abundances are low, the population is kept low by lower per capita survival. However, if stochastic events push relative abundance over a threshold, the population can abruptly increase to a new level. Thus, populations exhibit alternative states due to the feedback caused by frequency-dependent survival. If survival is low at low abundances, however, what prevents populations from going extinct? The answer is stochasticity itself. In the lottery model, stochasticity facilitates the coexistence of species by increasing the average population growth rate of rare species relative to common species. This occurs because, when abundant species experience a favorable year of high recruitment, they also experience high competition with conspecifics for vacant sites for seedling establishment. This increased intraspecific competition lowers the abundance of common species, leading to decreased effects of interspecific competition on rare species (Chesson and Warner 1981, Chesson 2000). Thus, even though rare species experience low survival probabilities in our model, they do not go extinct because stochasticity reduces the competition they experience from other species. Hence, stochasticity destabilizes communities in the sense of increasing the likelihood of large abrupt changes, but also stabilizes them by promoting species coexistence and limiting extinctions.

This combination of community stability and instability is closely consistent with the paleoecological record of Holocene tree dynamics in mesic eastern North American forests, and particularly for the subset of tree taxa that are mesic, shade-tolerant, late-successional species that might be expected to be most strongly governed by frequency-dependent self-reinforcing feedbacks. The composition of eastern North American forests has been largely stable between ~8,200 yr ago (collapse of the Laurentide Ice Sheet) and ~400 yr ago, with the onset of Euro-American land clearing (McAndrews 1988), with no recorded extirpations during this time interval and additions of tree taxa to landscape-scale species assemblages largely governed by post-glacial expansion of plant ranges (Woods and Davis 1989, Jackson and Booth 2002). However, superimposed upon this stability of forest composition is a strong second-order pattern of compositional instability and abrupt change (Booth et al. 2012*a*, Wang et al. 2016). The tree taxa with the best evidence for abrupt decline in the Holocene are mesic, late-successional, shade-tolerant trees: *T. canadensis*, *F. grandifolia*, and *Ulmus* in eastern North America (Booth et al. 2012*a*, Wang et al. 2016) and *Ulmus* and *Corylus avelana* in Europe (Shuman 2012). These trees establish microclimates

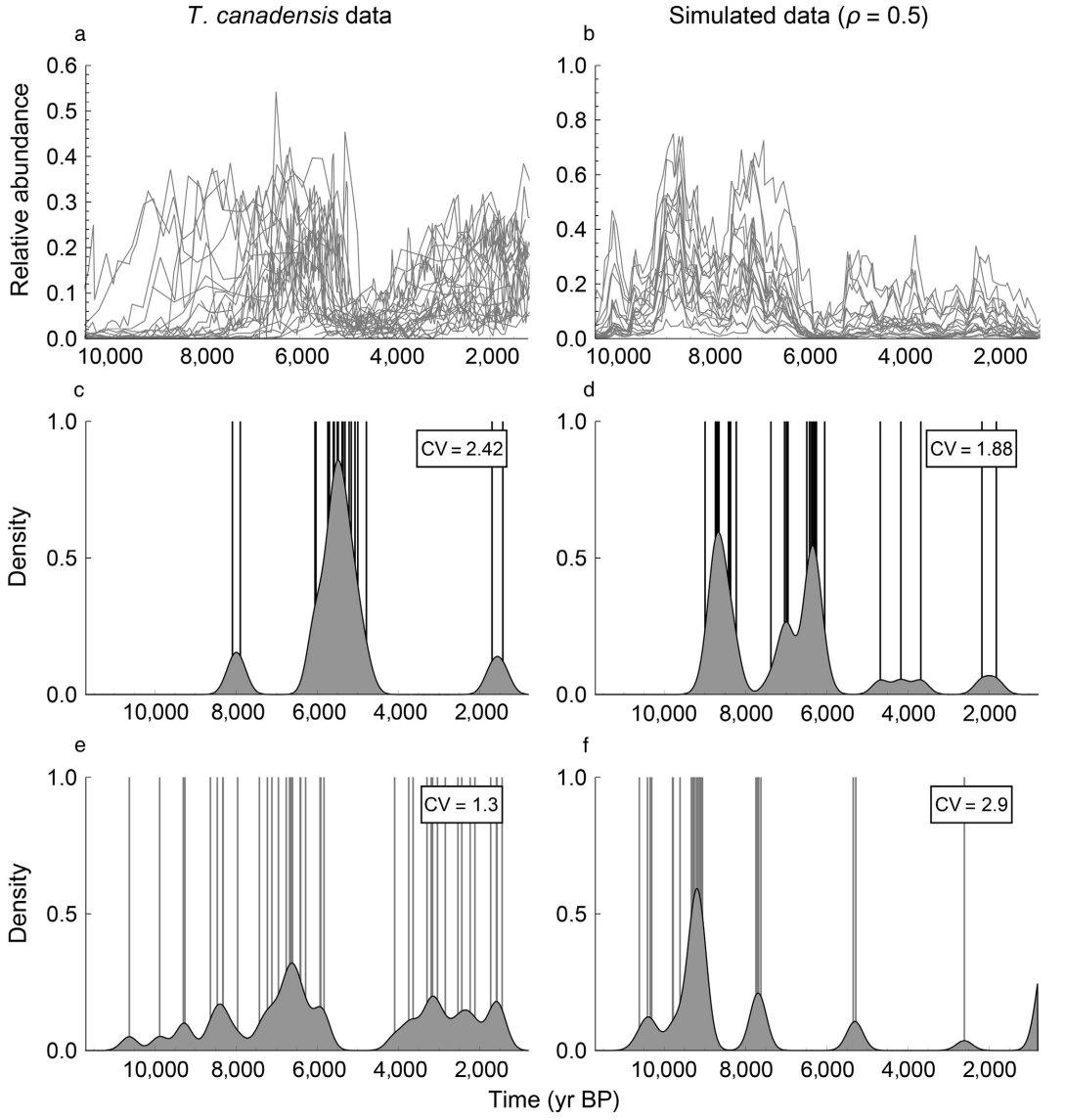

FIG. 5. (a, c, e) Quasi-synchrony of abrupt changes for the *Tsuga canadensis* data and (b, d, f) an example of simulated data with intermediate spatial environmental autocorrelation ($\rho = 0.5$). Panels a and b depict actual time series. The middle and bottom panels showed the distribution of abrupt decreases (black vertical lines; panels c and d) and increases (gray vertical lines; panels e and f). The smooth histograms represent the density of abrupt changes through time. Other parameters: $s = 0.3$, $\sigma = \sigma_1 = 0.7$, $f = 0$.

and moist soil litter that reduce the likelihood of fire and promote survival of juveniles (Burns and Honkala 1990*a*, *b*). Hence, it is ecologically plausible that these taxa are particularly subject to self-reinforcing feedbacks associated with frequency dependence in fecundity and survival. The resulting self-reinforcing feedback may accentuate past observed abrupt changes.

The apparent quasi-synchrony of the *T. canadensis* decline is often used as an argument for a large-scale change in the environment such as multi-centennial droughts or changes in surface air temperatures (Shuman 2012, Marsicek et al. 2013) or pest/pathogen outbreak (Davis 1981). These hypothesized extrinsic mechanisms remain viable and plausible. Nonetheless, spatial synchrony in population fluctuations are pervasive in nature and can arise from several mechanisms in addition to broad-scale and persistent environmental changes, such as dispersal and spatial autocorrelation of short-term environmental shocks (Walter et al. 2017). Using three different types of models, van Nes and Scheffer (2005) showed that increased dispersal can synchronize population collapse in a domino effect. This type of modeled behavior has led to the use of synchrony as an early warning of abrupt ecosystem changes (Dakos et al. 2010). Similarly, environmental stochasticity tends to synchronize population dynamics, known as the Moran effect, and is a

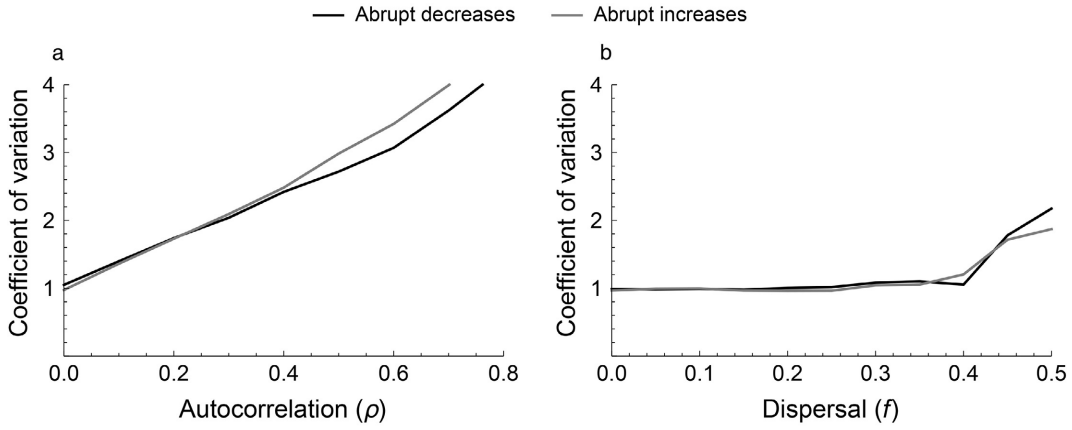

FIG. 6. Average increase in synchrony (represented by coefficient of variation) of abrupt decreases (black) and increases (gray), as (a) environmental autocorrelation increases and (b) dispersal increases for 100 replicates. Parameters: panel a, $s = 0.3$, $\sigma = \sigma_1 = 0.7$, $f = 0$; panel b, $s = 0.3$, $\sigma = \sigma_1 = 0.8$, $\rho = 0$.

dominant synchronizing mechanism (Hanski 1998). For instance, in a study of British moths and aphids across 21 localities up to 800 km apart, the Moran effect explains the spatial synchrony of each population better than dispersal (Hanski and Woiwod 1993). These synchronous dynamics can also increase the likelihood of regional population collapses (Chesson 1998).

Seed-dispersal effects appear to be less important for synchronizing abrupt changes at the regional scales considered here. In our model, collapses only become substantially synchronized when at least 40% of seeds disperse to adjacent cells during the 10-yr time step in the model (Fig. 6). Hence, dispersal of *T. canadensis* seeds is probably too limited to synchronize abrupt changes in reality, since estimates of typical *T. canadensis* seed dispersal are 40–400 m for individual dispersal events (Clark et al. 1999, He and Mladenoff 1999). On the other hand, the distances required for travel in the 10-yr period (50 km) is small compared to the 1,500 km over which this dispersal can synchronize abrupt changes. This suggests that dispersal could be a potent agent of synchronization at more localized scales. For example, *F. grandifolia* experienced multiple abrupt changes during the late Holocene (Wang et al. 2016), but these events appear to either be localized or to occur at sub-regional scales (e.g., upper Great Lakes; Booth et al. 2012*a*). Synchronization by seed dispersal could be more important for these more localized events.

One intriguing mismatch between observations and simulations is the differences in levels of clustering between abrupt increases and declines (Figs. 3–5). Whereas abrupt increases and decreases are generally symmetric in the simulations (Fig. 6), these events are asymmetric in the empirical data for *T. canadensis*, with abrupt decreases more synchronized than abrupt increases. In our model, abrupt increases are generated by the same processes as abrupt decrease, because synchronized abrupt decreases in one species are coupled with abrupt increases in one or both of the other species. This discrepancy – symmetry in the model, asymmetry in the data – suggests that the synchrony of abrupt decreases in *T. canadensis* is caused by some process that does not affect abrupt increases, or vice versa. This could be a signal of pathogen outbreaks (Davis 1981) being synchronized by environmental variability or could indicate that persistent environmental change might be a key factor in *T. canadensis* declines, for example, if multi-decadal- to centennial-scale droughts are required to trigger widespread increases in adult mortality. This asymmetry in clustering between abrupt declines and abrupt increases is an important signal in the data, and hence serves as a useful target for future model development and benchmarking.

In presenting our model, we have mainly focused on comparisons between the model and data from *T. canadensis*; however, our analyses of nine other tree taxa showed that abrupt changes were pervasive during the Holocene (Figs. 2, 3; Appendix S1). Among the 10 taxa, *T. canadensis* shows the strongest evidence for synchrony, but synchrony is apparent for several additional taxa (*Fagus* increases and *Ulmus* and *Picea* decline). However, other taxa show no evidence of synchrony, suggesting that abrupt changes for these taxa may be fully governed by intrinsic processes. An important challenge here is the uncertainty in the age models. While our results are based on the best estimate of synchrony given the current data, additional and more precise dates for individual sites would reduce uncertainty and better pinpoint the timing of abrupt changes, and ultimately enhance our understanding of the degree of synchrony. The ability to synchronize Holocene signals using cryptotephras is also promising (Pyne-O'Donnell et al. 2012, Spano et al. 2017). The ability to detect abrupt change may also be influenced by pollen representation, with a greater likelihood of missing abrupt ecological changes in underrepresented taxa. Overall, abrupt changes were common across the taxa considered here, but spatial and

temporal heterogeneities among taxa suggest that explaining abrupt changes should not be limited to the traditional search for climatic or other broad-scale extrinsic drivers (Jeffers et al. 2015).

We used a process-based model to explore the role of intrinsic processes (specifically, frequency-dependent survival) in patterns of abrupt changes through time and space, focusing on the case of symmetrical interactions among species to highlight the role of intrinsic processes. An alternative modeling approach would be to include a larger number of species governed by different demographic parameters or other traits distributed in a spatially and temporally heterogeneous environment (Blaauw et al. 2010). Such a model could potentially be statistically fit to multiple time-series such as the time series data we have presented (Jeffers et al. 2011*a*, *b*, 2015). A key challenge to such approaches is the scarcity of colocated paleohydrological proxy data for the Holocene (Marlon et al. 2017), although this is improving, particularly for the last two millennia (Rodysill et al. 2018, Shuman et al. 2018). An additional challenge is the simultaneous statistical fitting of multiple taxa from multiple sites, accounting for potential differences among taxa and, for the same taxon, differences in dynamics among sites. This approach will likely contribute valuable insights into the temporal and spatial patterns of abrupt changes among taxa throughout the Holocene, and it will also likely further highlight the possible role of intrinsic processes in driving these abrupt changes.

Conclusion

Understanding the causes of abrupt ecological changes is important, because many ecological systems are expected to change abruptly, with negative consequences for human society, when they are subjected to increasing rates and magnitudes of global change (Barnosky et al. 2012, Steffen et al. 2015, Ratajczak et al. 2018). Paleoecology provides an opportunity to understand dynamics of past ecological systems, to identify past causes of abrupt change, and to use this information to assess and predict the vulnerability of contemporary ecosystems to abrupt change (Shuman 2012, Seddon et al. 2015; Williams and Burke, 2019). Our work has illustrated different processes that may generate abrupt and quasi-synchronous changes in past forests. Abrupt changes in forest composition, both increases and decreases, can be caused or accentuated by intrinsic processes such as frequency-dependent survival. These processes generate abrupt changes and suggest that past abrupt change and community state shifts at local to regional scales could have been triggered solely by single, short-term environmental shocks (e.g., a single unfavorable year or decade). Intrinsic processes that generate self-reinforcing feedbacks are likely to be pervasive in natural communities, and more work is needed to incorporate these processes into the modeling and analysis of past abrupt changes documented in paleorecords.

Acknowledgments

We thank the data contributors and data stewards to the Neotoma Paleoecology Database, two anonymous reviewers, and the ACES group at the University of Wisconsin-Madison. This work was supported by a UW2020 award from the Wisconsin Alumni Research Foundation. J. W. Williams was also supported by NSF (144-PRJ82RZ, 144-AAB2562).

Literature Cited

Allison, T. D., R. E. Moeller, and M. B. Davis. 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. Ecology 67:1101–1105.

Barnosky, A. D., et al. 2012. Approaching a state shift in Earth's biosphere. Nature 486:52–58.

Barry, D., and J. A. Hartigan. 1993. A Bayesian-analysis for change point problems. Journal of the American Statistical Association 88:309–319.

Bennett, K. D., and J. L. Fuller. 2002. Determining the age of the mid-Holocene *Tsuga canadensis* (hemlock) decline, eastern North America. Holocene 12:421–429.

Blaauw, M., K. D. Bennett, and J. A. Christen. 2010. Random walk simulations of fossil proxy data. Holocene 20:645–649.

Blois, J. L., J. W. Williams, E. C. Grimm, S. T. Jackson, and R. W. Graham. 2011. A methodological framework for assessing and reducing temporal uncertainty in paleovegetation mapping from late-Quaternary pollen records. Quaternary Science Reviews 30:1926–1939.

Booth, R. K., S. Brewer, M. Blaauw, T. A. Minckley, and S. T. Jackson. 2012*a*. Decomposing the mid-Holocene *Tsuga* decline in eastern North America. Ecology 93:1841–1852.

Booth, R. K., S. T. Jackson, V. A. Sousa, M. E. Sullivan, T. A. Minckley, and M. J. Clifford. 2012*b*. Multi-decadal drought and amplified moisture variability drove rapid forest community change in a humid region. Ecology 93:219–226.

Burns, R., and B. Honkala. 1990*a*. Silvics of North America. Volume 1. Conifers. Forest Service, United States Department of Agriculture, Washington, D.C., USA.

Burns, R., and B. Honkala. 1990*b*. Silvics of North America. Volume 2. Hardwoods. Forest Service, United States Department of Agriculture, Washington, D.C., USA.

Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecological Applications 9:751–771.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments—a look at the combined effects of different sorts of variability. Theoretical Population Biology 28:263–287.

Chesson, P. L. 1998. Making sense of spatial models in ecology. Pages 151–166 *in* J. Bascompte, and R. V. Solé, editors. Modeling spatiotemporal dynamics in ecology. Landes Bioscience, Austin, Texas, USA.

Chesson, P. L. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. American Naturalist 117:923–943.

Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. American Naturalist 152:204–224.

Clark, J. S., and J. S. McLachlan. 2003. Stability of forest biodiversity. Nature 423:635–638.

Clark, J. S., M. R. Silman, R. Kern, E. Macklin, and J. H. R. Lambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80:1475–1494.

Dakos, V., E. H. van Nes, R. Donangelo, H. Fort, and M. Scheffer. 2010. Spatial correlation as leading indicator of catastrophic shifts. Theoretical Ecology 3:163–174.

Davis, M. B. 1981. Outbreaks of forest pathogens in quaternary history. IV International Palynology Conference, Lucknow 3: 216–228.

Dawson, A., C. J. Paciorek, J. S. McLachlan, S. Goring, J. W. Williams, and S. T. Jackson. 2016. Quantifying pollen-vegetation relationships to reconstruct ancient forests using 19th-century forest composition and pollen data. Quaternary Science Reviews 137:156–175.

Erdman, C., and J. W. Emerson. 2007. bcp: an R package for performing a Bayesian analysis of change point problems. Journal of Statistical Software 23:1–13.

Erdman, C., and J. W. Emerson. 2008. A fast Bayesian change point analysis for the segmentation of microarray data. Bioinformatics 24:2143–2148.

Foster, D. R., W. W. Oswald, E. K. Faison, E. D. Doughty, and B. C. S. Hansen. 2006. A climatic driver for abrupt mid-Holocene vegetation dynamics and the hemlock decline in New England. Ecology 87:2959–2966.

Goring, S., A. Dawson, G. L. Simpson, K. Ram, R. W. Graham, E. C. Grimm, and J. W. Williams. 2015. Neotoma: a programmatic interface to the Neotoma Paleoecological Database. Open Quaternary 1:Art. 2.

Goring, S., J. W. Williams, J. L. Blois, S. T. Jackson, C. J. Paciorek, R. K. Booth, J. R. Marlon, M. Blaauw, and J. A. Christen. 2012. Deposition times in the northeastern United States during the holocene: establishing valid priors for Bayesian age models. Quaternary Science Reviews 48:54–60.

Hanski, I. 1998. Metapopulation dynamics. Nature 396:41–49.

Hanski, I., and I. P. Woiwod. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology 62:656–668.

Haslett, J., and A. Parnell. 2008. A simple monotone process with application to radiocarbon-dated depth chronologies. Journal of the Royal Statistical Society: Series C (Applied Statistics) 57:399–418.

He, H. S., and D. Mladenoff. 1999. The effects of seed dispersal on the simulation of long-term forest landscape change. Ecosystems 2:308–319.

Henne, P. D., C. M. Elkin, B. Reineking, H. Bugmann, and W. Tinner. 2011. Did soil development limit spruce (*Picea abies*) expansion in the central Alps during the Holocene? Testing a palaeobotanical hypothesis with a dynamic landscape model. Journal of Biogeography 38:933–949.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Ives, A. R., A. Einarsson, V. A. A. Jansen, and A. Gardarsson. 2008. High-amplitude fluctuations and alternative dynamical states of midges in lake Myvatn. Nature 452:84–87.

Jackson, S. T., J. L. Betancourt, R. K. Booth, and S. T. Gray. 2009. Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. Proceedings of the National Academy of Sciences USA 106:19685–19692.

Jackson, S. T., and R. K. Booth. 2002. The role of late holocene climate variability in the expansion of yellow birch in the western great lakes region. Diversity and Distributions 8:275–284.

Jeffers, E. S., M. B. Bonsall, S. J. Brooks, and K. J. Willis. 2011*a*. Abrupt environmental changes drive shifts in tree–grass interaction outcomes. Journal of Ecology 99:1063–1070.

Jeffers, E. S., M. B. Bonsall, and K. J. Willis. 2011*b*. Stability in ecosystem functioning across a climatic threshold and contrasting forest regimes. PLoS ONE 6:e16134.

Jeffers, E. S., M. B. Bonsall, C. A. Froyd, S. J. Brooks, and K. J. Willis. 2015. The relative importance of biotic and abiotic processes for structuring plant communities through time. Journal of Ecology 103:459–472.

Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. Ecology 77:2027–2042.

Marlon, J. R., et al. 2017. Climatic history of the northeastern United States during the past 3000 years. Climate of the Past 13:1355–1379.

Marsicek, J. P., B. Shuman, S. Brewer, D. R. Foster, and W. W. Oswald. 2013. Moisture and temperature changes associated with the mid-Holocene *Tsuga* decline in the northeastern United States. Quaternary Science Reviews 80:129–142.

May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477.

McAndrews, J. 1988. Human disturbances of North American forests and grasslands: the fossil pollen record. Volume 7. Springer, Dordrecht, The Netherlands.

Moorcroft, P. R., S. W. Pacala, and M. A. Lewis. 2006. Potential role of natural enemies during tree range expansions following climate change. Journal of Theoretical Biology 241:601–616.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

Nieto-Lugilde, D., K. C. Maguire, J. L. Blois, J. W. Williams, and M. C. Fitzpatrick. 2015. Close agreement between pollen-based and forest inventory-based models of vegetation turnover. Global Ecology and Biogeography 24:905–916.

Ordonez, A., and J. W. Williams. 2013. Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. Ecology Letters 16:773–781.

Parnell, A., 2014. Bchron: radiocarbon dating, age-depth modelling, relative sea level rate estimation, and non-parametric phase modelling. R package version 4.1, 1.

Pyne-O'Donnell, S. D., et al. 2012. High-precision ultra-distal Holocene tephrochronology in North America. Quaternary Science Reviews 52:6–11.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Ranta, E., V. Kaitala, and J. Lindstrom. 1999. Spatially autocorrelated disturbances and patterns in population synchrony. Proceedings of the Royal Society B: Biological Sciences 266:1851–1856.

Ratajczak, Z., S. R. Carpenter, A. R. Ives, C. J. Kucharik, T. Ramiadantsoa, M. A. Stegner, J. W. Williams, J. Zhang, and M. G. Turner. 2018. Abrupt change in ecological systems: inference and diagnosis. Trends in Ecology & Evolution 33:513–526.

Reimer, P. J., et al. 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1869–1887.

Rodysill, J. R., et al. 2018. A North American hydroclimate synthesis (NAHS) of the Common Era. Global and Planetary Change 162:175–198.

Saltré, F., R. Saint-Amant, E. Gritti, S. Brewer, C. Gaucherel, B. Davis, and I. Chuine. 2013. Climate or migration: what limited European beech post-glacial colonization? Global Ecology and Biogeography 22:1217–1227.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology & Evolution 18:648–656.

Seddon, A. W. R., C. A. Froyd, A. Witkowski, and K. J. Willis. 2014. A quantitative framework for analysis of regime shifts in a Galapagos coastal lagoon. Ecology 95:3046–3055.

Seddon, A. W. R., M. Macias-Fauria, and K. J. Willis. 2015. Climate and abrupt vegetation change in Northern Europe since the last deglaciation. Holocene 25:25–36.

Shuman, B. 2012. Patterns, processes, and impacts of abrupt climate change in a warm world: the past 11,700 years. Wiley Interdisciplinary Reviews: Climate Change 3:19–43.

Shuman, B. N., P. Newby, and J. P. Donnelly. 2009. Abrupt climate change as an important agent of ecological change in the Northeast US throughout the past 15,000 years. Quaternary Science Reviews 28:1693–1709.

Shuman, B. N., C. Routson, N. McKay, S. Fritz, D. Kaufman, M. E. Kirby, N. Connor, G. T. Pederson, and J.-M. St-Jacques. 2018. Placing the Common Era in a Holocene context: millennial to centennial patterns and trends in the hydroclimate of North America over the past 2000 years. Climate of the Past 14:665.

Spano, N., C. S. Lane, S. Francis, and T. Johnson. 2017. Discovery of Mount Mazama cryptotephra in Lake Superior (North America): implications and potential applications. Geology 45:1071–1074.

Staver, A. C., and S. A. Levin. 2012. Integrating theoretical climate and fire effects on savanna and forest systems. American Naturalist 180:211–224.

Steffen, W., et al. 2015. Planetary boundaries: guiding human development on a changing planet. Science 347:1259855.

Sugita, S. 2007. Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition. Holocene 17:229–241.

Umbanhowar, C. E., P. Camill, C. E. Geiss, and R. Teed. 2006. Asymmetric vegetation responses to mid-Holocene aridity at the prairie–forest ecotone in south-central Minnesota. Quaternary Research 66:53–66.

Usinowicz, J. 2015. Limited dispersal drives clustering and reduces coexistence by the storage effect. American Naturalist 186:634–648.

van Nes, E. H., and M. Scheffer. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. Ecology 86:1797–1807.

Walter, J. A., L. W. Sheppard, T. L. Anderson, J. H. Kastens, O. N. Bjornstad, A. M. Liebhold, and D. C. Reuman. 2017. The geography of spatial synchrony. Ecology Letters 20:801–814.

Wang, X., and J. W. Emerson. 2015. Bayesian change point analysis of linear models on graphs. arXiv preprint arXiv: 1509.00817.

Wang, Y., J. L. Gill, J. Marsicek, A. Dierking, B. Shuman, and J. W. Williams. 2016. Pronounced variations in *Fagus grandifolia* abundances in the Great Lakes region during the Holocene. Holocene 26:578–591.

Webb, I. T. 1993. Constructing the past from late-Quaternary pollen data: temporal resolution and a zoom lens space-time perspective. Pages 79–101 *in* S. M. Kidwell and A. K. Behrensmeyer, editors. Taphonomic approaches to time resolution in fossil assemblages. Paleontological Society, Knoxville, Tennessee, USA.

Williams, J. W., J. L. Blois, and B. Shuman. 2011. Extrinsic and intrinsic forcing of abrupt ecological change: case studies from the late Quaternary. Journal of Ecology 99:664–677.

Williams, J. W., and K. Burke. 2019. Past abrupt changes in climate and terrestrial ecosystems. Pages 128–141 *in* T. Lovejoy and L. Hannah, editors. Climate change and biodiversity: Transforming the Biosphere. Yale Univ Press, New Haven, CT.

Williams, J. W., et al. 2018. The neotoma paleoecology database, a multiproxy, international, community-curated data resource. Quaternary Research 89:156–177.

Williams, J. W., B. Shuman, and P. J. Bartlein. 2009. Rapid responses of the prairie-forest ecotone to early Holocene aridity in mid-continental North America. Global and Planetary Change 66:195–207.

Wolfram Research, Inc. 2017. Mathematica, version 11.2. Wolfram Research, Inc., Champaign, Illinois, USA.

Woods, K. D., and M. B. Davis. 1989. Paleoecology of range limits: beech in the upper peninsula of Michigan. Ecology 70:681–696.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2579/suppinfo

Data Availability

Code are available on Zenodo: https://doi.org/10.5281/zenodo.1576951