Nonlinear tree growth dynamics predict resilience to disturbance

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Abstract. Following a disturbance, why does one tree survive while another dies? Physiological mechanisms may explain varying responses to disturbance between different tree species, but fewer studies have investigated conspecific variation in resilience to forest disturbance. We propose that a dynamic signal found in trees may provide clues to their post-disturbance fate. Specifically, linear versus nonlinear growth dynamics of a tree may be an indicator of its likelihood to survive a disturbance. Here, we investigate stands of red oak (*Quercus rubra* L.) that experienced disturbances in the form of drought and insect attack. Earlier work indicated that oaks dying during these disturbances had faster growth rates in their first years of life, but there was no obvious difference in canopy status, size, age, or microsite habitat between trees that survived and those that died. To investigate potential differences in growth dynamics between these trees, we quantified radial growth of individual trees and used two forecasting models to classify tree growth dynamics as linear or nonlinear. Trees were classified as healthy, declining, or dying based on crown cover, and dynamic patterns of growth were related to these health classifications. Contrary to expectations, we found healthy *Q. rubra* were significantly more likely to exhibit nonlinear growth dynamics relative to declining and dying trees. The drivers of this effect remain unclear, but nonlinear growth dynamics in healthy trees may represent an enhanced ability to benefit from resource pulses, in turn promoting greater resilience. Our work suggests that forecasting models offer a means of predicting tree survival during forest disturbances and thus represent an increasingly valuable tool as forest disturbances increase in frequency and severity.

Key words: dendrochronology; disturbance; drought; insect outbreaks; nonlinear forecasting models; radial growth; red oak borer; tree population dynamics; tree rings.

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INTRODUCTION

Ecosystems can exhibit strong responses to disturbance events, which are defined broadly as periodic interferences in the availability of resources, substrate or environmental conditions that impact the system's ecological functioning (White and Pickett 1985). Whether and why an ecosystem exhibits either resistance or resilience to a disturbance has been a subject of ecological study for decades (Holling 1973, Folke et al. 2004). Projections of increasing frequency and severity of disturbance events linked to anthropogenic climate change (Adams et al. 2009, IPCC

2013) have prompted a proliferation of recent studies exploring these issues, particularly in forests (e.g., Stephen et al. 2001, Breshears et al. 2005, Haavik et al. 2011, Haavik et al. 2012, Scheffer et al. 2012, Clark et al. 2014, Filotas et al. 2014, Jones et al. 2014). Many forests already appear to be experiencing increasing frequency of disturbance (Dale et al. 2001) with related tree mortality due to land use change, pollution, and apparently natural events like drought, wind-throw, and pest infestations (Hanson and Weltzin 2000, Ulanova 2000, Dale et al. 2001, Haavik et al. 2008). Because of forests' capacity to feedback to climate (Adams et al. 2009) and their inherent economic, habitat, recreational, and aesthetic values (Bonan 2008), predicting how forested systems will respond to disturbances is an important societal goal.

In spite of the importance of accurate predictions of forest response to disturbance, such predictions remain problematic. The spectrum of potential forest responses to disturbance is broad, ranging from catastrophic regime shift (Scheffer et al. 2001) to far subtler responses such as the alteration of tree productivity (Ciais et al. 2005). Between these extremes, many forests are resilient, experiencing widespread tree mortality in response to disturbance while still maintaining their basic functioning as forested ecosystems (Holling and Gunderson 2002, Breshears et al. 2005, Small et al. 2005, McDowell et al. 2010), sometimes with tree species composition similar to the pre-disturbance ecosystem (Haavik et al. 2012, Knapp et al. 2013). For forests that do not experience a regime shift in spite of widespread mortality, tools for predicting how they might fare in response to disturbance are generally limited to characterizing species' distinct physiological responses to specific disturbance types, and using those physiological parameters to predict which trees might exhibit resilience.

Recent regional-scale forest disturbances, many characterized by drought, offer opportunities to test species-specific, physiological tools. For example, investigators have elucidated distinct physiological responses of different co-occurring tree genera (Breshears et al. 2005, 2009, Eilmann and Rigling 2012, Mitchell et al. 2013) and co-occurring oak species (Hu et al. 2013, Renninger et al. 2014) to drought. Such studies help investigators predict which tree

species may be relatively resilient to this type of disturbance. Fewer studies explore variation in response to disturbance across individuals within a population. Though it might appear reasonable to assume that intra-species variation in disturbance response is smaller than inter-species variation, especially when variation in resource availability across microsites is controlled, some studies suggest otherwise. For example, growing evidence suggests that intra-specific variation in response to environmental conditions can be as great as or greater than variation across species (Clark et al. 2004, Clark 2010). Other studies suggest that varied responses to environmental conditions within a species can be linked to survival post-disturbance. Sevanto et al. (2014) highlight how individuals of one pine species (piñon pine, *Pinus edulis*) can exhibit distinct strategies for coping with drought that, in turn, appear linked to survival time during persistent drought. Similarly, variation in conspecific tree-ring width early in life has been linked to tree survival during an insect outbreak (Haavik et al. 2011).

These examples suggest that a meaningful degree of variation in response to disturbance can occur within some species that is unrelated to microsite differences, but rather reflects inherent variation in functioning among individuals. If so, this phenomenon might be an important feature driving patterns of within-species tree mortality following disturbance. Such patterns prompt basic questions about trees' susceptibility to disturbance: why might some trees in a population subjected to a disturbance die, while others survive, especially among intermingled, co-occurring trees with apparently similar access to resources? Aside from the physiologically-based approaches described above that are typically relevant only for a select disturbance type (e.g., drought), few tools exist to address this intriguing and important question.

One clue might lie in the dynamic signal found in metrics of tree growth. Tree-ring growth indices reflect a tree's bole growth response to the environment. If we assume that bole growth is indicative of tree growth more generally, as is the norm in dendrochronology studies (Speer 2010), and that sampled trees adequately represent the dominant forest species, such indices would be broadly representative of forest growth

responses to environmental change. These growth responses over time may be particularly useful given recent advances in our understanding of forests as dynamical, complex systems (De Grandpré et al. 2009). Work in a multitude of complex systems suggests that the presence of nonlinear dynamics, whereby small differences in driving conditions can result in divergent system responses (Lorenz 1963), may be an indicator of disturbance or stress and increase the likelihood of system collapse (Berryman 1991, Jing et al. 2003, Mullon et al. 2005, Anderson et al. 2008, Vandermeer and Lin 2008, Glaser et al. 2014). These studies contrast with work indicating that nonlinear behaviors are linked to greater survival of human neonates (Sugihara et al. 1996); the mechanisms driving these contrasts remain unclear. If linkages between nonlinear growth dynamics and eventual collapse observed in a variety of other systems (e.g., Berryman 1991, Jing et al. 2003, Mullon et al. 2005, Vandermeer and Lin 2008) are robust in forests, the detection of such behavior could be a useful means of beginning to understand why some trees die while other survive and, more broadly, for predicting a forest's response to disturbance. This may be particularly valuable given that tree cores, and thus tree-ring indices from multiple years' growth, are readily obtainable.

We investigate whether the presence of nonlinear dynamics in growth of tree populations subjected to disturbance could serve as a predictor of disturbance-related mortality. If so, detecting historical tree growth dynamics using tree cores may provide a rapid means of predicting the fate of a forest stand during a disturbance. In this context, nonlinear refers to tree radial growth patterns reflecting variable responses to environmental cues, as opposed to linear patterns that reflect more constitutive growth as the environment changes. Though the behavior of nonlinear dynamical systems is by definition difficult to predict, particularly over long time frames (Glaser et al. 2014), systems exhibiting nonlinear dynamics possess qualities that may permit an investigator to assess their sustainability: their very complexity may lend itself to predicting their fate in response to disturbance. We explored the relationship between tree response to disturbance and temporal dynamics of historic tree growth using a recent,

regional-scale, oak decline event in northwest and west-central Arkansas, USA. The decline and eventual mortality of a significant fraction of red oaks (*Quercus* subgenus *Erythrobalanus*) in these forests has been linked to cyclical droughts in the 1950s and 1960s and subsequent wood-boring insect outbreaks (Haavik et al. 2012). After two severe droughts, wood-boring insect populations began to increase in the mid-1970s. Severely infested trees experienced declines in growth rates, and many of these trees eventually experienced mortality in the early 21st century (Haavik and Stephen 2010). Though all trees' growth responded in a similarly positive manner to a calculated index of historical moisture availability, trees most susceptible to this disturbance event exhibited greater growth rates early in their lives relative to trees that survived (Haavik et al. 2011). The association between faster growth early in life and mortality during a disturbance is consistent with genetically-based growth strategies influencing differences in survival (Johnson and Abrams 2009), and prompted us to ask if dynamical signals differed in tree-ring growth patterns between dying and surviving trees.

We use this disturbance event, the juxtaposition of surviving and dying trees following the disturbance, and the availability of time-series, tree growth data to assess the degree to which antecedent tree growth dynamics are linked to tree survival after a disturbance. Consistent with studies indicating that nonlinear dynamics can be linked to population collapse (Berryman 1991, Jing et al. 2003, Mullon et al. 2005, Vandermeer and Lin 2008), we hypothesized that trees experiencing mortality post-disturbance would exhibit nonlinear growth dynamics, and that linear growth dynamics would be exhibited by trees apparently resistant to the disturbance event. Testing this hypothesis cannot discern the mechanism driving tree survival or susceptibility to disturbance. However, unlike more mechanistic studies exploring trees' physiological response to a particular disturbance type (Breshears et al. 2005, 2009, Eilmann and Rigling 2012, Hu et al. 2013, Mitchell et al. 2013, Renninger et al. 2014), our approach is applicable to a multitude of disturbance types. We use the results of our work to begin to disentangle the mystery of why some trees appear susceptible to

disturbance, while conspecifics with apparently similar access to resources and co-dominance status in the canopy succumb. Our work can guide future, more mechanistic studies critical for predicting trees' probability of survival during disturbance events.

METHODS

Study sites

The study relied on ring width indices of *Q. rubra* radial growth developed from the Boston Mountains (24 trees) and the Ouachita Mountains (46 trees), two forested regions in northwestern and west-central Arkansas, USA that experienced widespread oak mortality during a red oak borer (*Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae)) outbreak. These are the same stands in which previous work indicated that *Q. rubra* growing the fastest during their youth were most susceptible to the recent insect disturbance (Haavik et al. 2011). The sites are characterized by deep valleys, steep ledges, and cliffs with elevations ranging from 370 to 700 m and rock formations of limestone, sandstone, and shale (Fenneman 1938, Adamski et al. 1995). Mean annual temperature for both regions is 16°C. They experience hot summers and mild winters, with an average summer high of 32°C and an average winter low of −1.3°C. Average precipitation totals 1240 mm in the Boston Mountains and 1500 mm in the Ouachita Mountains, with most precipitation occurring during spring and fall (National Climatic Data Center 2009). Site quality for *Q. rubra* in the region is primarily determined by the depth and texture of the A horizon. Soils are fine sandy loams in the Boston Mountains and shallow, permeable loams in the Ouachita Mountains (Soil Survey 2012), and are generally rocky, with low organic matter content.

Tree-ring sampling and analysis

Tree radial growth is an integrated measure of many factors influencing the annual carbon source and sink dynamics of a tree (Schweingruber 1996), and therefore often is employed to understand tree growth, ecosystem function, and population dynamics. As such, established methodologies exist for quantifying radial growth across time (Douglass 1941). Using these methods as a guide, we measured ring widths for four radii located along each of the four cardinal directions for each of 24 cross-sectional slabs (ca. 5 cm thick) from trees felled in 2007 in the Boston Mountains, and from two radii located along the east and west axes for each of 46 cores from trees felled in 2009 in the Ouachita Mountains. Minor directional adjustments were made if reaction wood was encountered (Fritts 1976). We sampled trees that were close neighbors (i.e., either immediately adjacent or within ~3 m) and ensured as much as possible that differences in canopy status and evident rooting conditions among sampled trees were minimized. All sampled trees were broadly representative of other red oaks in the stand. We averaged these ring width measurements to derive one tree-ring growth series per tree (Fig. 1). We consider averaged tree-ring growth series as an indicator of incremental, annual bole growth; though this approach cannot account for growth of branches, foliage, or roots, the approach permits valuable inferences about tree growth over time (Speer 2010). Importantly, because oaks are ring-porous trees, they form relatively large earlywood vessels early in each growing season, making missing rings unlikely and each ring easy to discern (Zimmermann 1983, Abrams 1990).

We assigned each sampled tree to one of three health status classifications. In the Boston Mountains the classification integrated percent crown dieback and abundance of wood-boring insect scars (Fierke et al. 2005). In the Ouachita Mountains, tree health was classified using percent crown cover. We defined health status as *healthy* in trees with percent crown dieback 1% or percent crown cover 99%; *declining* in trees experiencing moderate levels of woodboring insect infestation and crown dieback or percent crown cover of 33–66%; and *dying* in trees experiencing high levels of boring insect infestations and crown dieback >66% or percent crown cover <44% (Fierke et al. 2005).

We measured annual ring width using Image-J software (Rasband 1997–2005), and standardized these raw measures (mean = 1.0) to generate ring-width indices (R) for each tree (Fritts 1976). Further details on the adapted methods are provided in Haavik et al. (2008) and Haavik et al. (2011). We provided average radii measurements for each tree to ARSTAN (Cook and
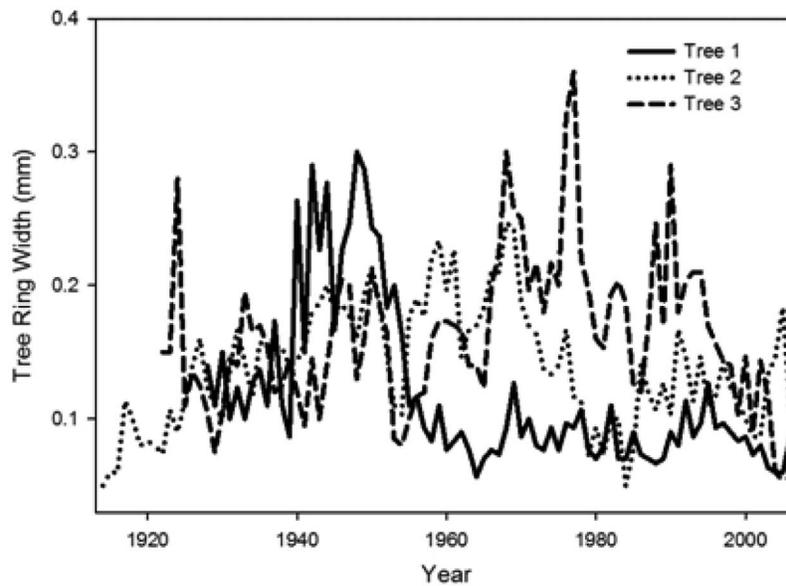
Fig. 1. Tree ring growth series with raw ring width (mm) plotted across time. Data presented are representative of a random sample of tree rings from the tree populations described in the text.

Holmes 1986), a freely-available program that develops standardized, individual tree-ring series. We analyzed six healthy, nine declining, and nine dying, well-interspersed, neighboring trees from the Boston Mountains, and 24 healthy, nine declining, and 13 dying, well-interspersed, neighboring trees from the Ouachita Mountains. Each tree-ring growth series represented at least 50 years of growth, but no tree was older than 100 years.

Nonlinear time series forecasting models

Nonlinear forecasting models are one method of detecting nonlinear dynamics in systems for which the structural form of a mechanistic model is unknown. This modeling approach has been applied in dynamic systems ranging from biological (Sugihara et al. 1996, Hsieh et al. 2005, Glaser et al. 2011) and astronomic (Kilcik et al. 2009) to economic (Schittenkopf 2000). We used a theoretical framework developed in Sugihara and May (1990) and Sugihara (1994) to characterize dynamic signatures in tree-ring time series, and we related these signatures to the health status of co-occurring tree populations. A mathematical description of these models can be found in numerous publications (e.g., Sugihara and May 1990, Sugihara 1994, 2012, Sugihara et

al. 1996, Hsieh et al. 2005, Glaser et al. 2011, 2014). An R package for implementing the methods is available at https://github.com/ha0ye/rEDM.

The term 'nonlinear' can have different but related meanings depending on its use. For example, the discrete logistic model is a nonlinear model insofar as its output is not linearly proportional to its input. However, depending on the choice of intrinsic growth rate (r) in the model, the resulting dynamics may reflect linearity (equilibrium), stable limit cycles, or chaos (May 1974). We adopt here a definition of nonlinear that applies to time-evolving dynamics (Tong 1993): *nonlinear dynamics* describe "time series that lack a symmetrical waveform and, as such, cannot be well described as sums of sine and cosine functions" (Sugihara et al. 1996). By this definition, stable limit cycles are not an example of nonlinear dynamics even if they represent a function whose output is not proportional to its input, but chaotic dynamics resulting from small differences in initial conditions (Lorenz 1963) are nonlinear.

We classified tree-ring growth over time as linear or nonlinear using the forecasting model S-map (Sugihara 1994). First, we estimated the dimensionality of the time series using a related
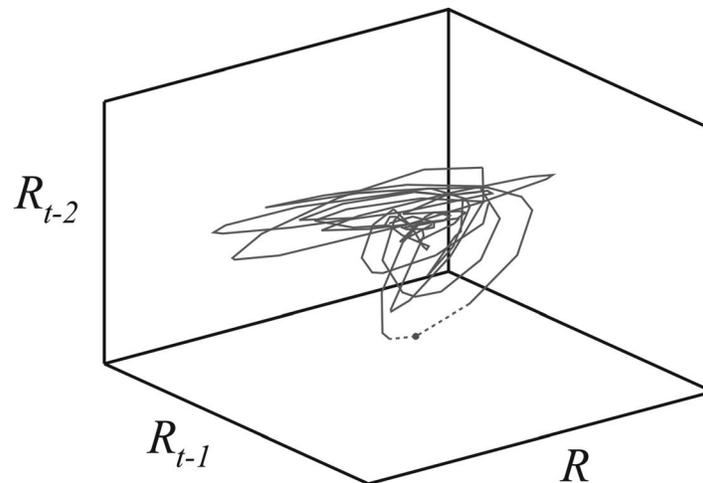
Fig. 2. Hypothetical example of a lagged coordinate embedding used to reconstruct system dynamics (state space reconstruction) to facilitate simplex projection and S-map modeling. The model, an attractor, is constructed by plotting consecutive lags at various time steps (t) (R_t, R_{t-1}, R_{t-2}) of the system variable in question (here, tree radial growth represented by R). The number of axes (and therefore number of time lags used) equals the embedding dimension, E, of the state space. Each coordinate in the attractor is therefore a vector of length E that is used to create library and prediction vectors for our two forecasting models. In our approach, the model is built from a set of library vectors (joined by solid lines) used to forecast one prediction vector (the dot, located along the dashed line).

method, simplex projection (Sugihara and May 1990). Dimensionality, which is related to the number of driving variables (e.g., temperature and rainfall) that structure system dynamics (i.e., tree-ring growth; Whitney 1936, Deyle and Sugihara 2011), is estimated by deconstructing a time series into E consecutive points (Takens 1981; Fig. 2). We selected the best E for each time series by varying E from 1 to 10, producing a series of forecasts of radial growth R, and comparing the observed values of R to model-produced forecasts using the Pearson correlation coefficient (ρ) and mean absolute error (MAE). While E could theoretically be higher than 10, following Glaser et al. (2014) we restricted our analysis to $E \leq 10$ because of the length of our time series; for a time series of length 60 years, an E of 10 results in only 6 vectors to use for forecasting, and exceeding vector lengths of 10 further reduces the number of vectors available. We used the model, or attractor (Fig. 2), of dimension E that produced forecasts with the lowest MAE and highest ρ to define system dimensionality. That dimensionality was then used as an input to S-map modeling to define the

shape of the dynamic attractor in the data.

S-map models classify system dynamics as linear or nonlinear by comparing a linear versus nonlinear model of the time series, and revealing the model that produces the best out-of-sample forecasts of R (Sugihara 1994, Hsieh et al. 2005, Glaser et al. 2014). First, the system attractor was reconstructed using a dimensionality of E measured by simplex projection. Second, a tuning parameter in the model, θ, was tuned from linear ($\theta = 0$) to nonlinear ($\theta > 0$ in steps of 0.1, up to $\theta = 10$). To assess whether a nonlinear model exhibited significantly improved forecasting ability compared to a linear model, we assigned a P value to the improvement in MAE of the nonlinear model over the linear model (ΔMAE) using a randomization procedure outlined in Hsieh and Ohman (2006). As in simplex projection, the best model of system dynamics was chosen by comparing observed to forecast values using statistics of ρ and MAE. In both simplex projection and S-map modeling, we analyzed standardized (mean = 0, standard deviation = 1), first differenced time series ($R_{t+1} - R_t$, where t is time) to reduce the effects of autocorrelation on
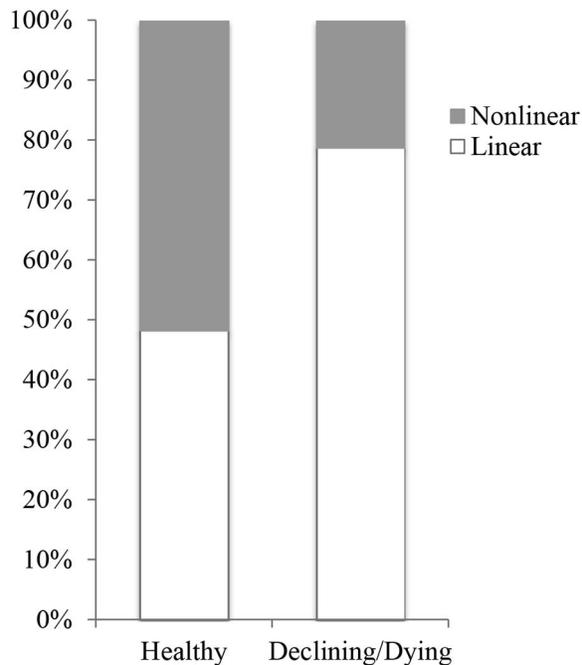
Fig. 3. S-map-classified dynamics from healthy and declining or dying trees from red oaks in Arkansas, USA. Healthy trees were significantly more likely to have nonlinear dynamics ($p = 0.015$). Analysis shown here combines declining and dying trees into one unhealthy class.

modeling. Models were built from a subset of 'library' vectors, and forecast metrics were calculated from a distinct, prediction set of vectors withheld from the model, permitting production of true, out-of-sample forecasts.

Linking growth dynamics to tree resilience

We employed logistic regression (R Core Team 2013; v.2.15.2) to test for a relationship between the *health class* of a tree and the *classification of dynamics* (linear or nonlinear). Only those time series that produced statistically significant S-map models (ρ_{max} corresponding to p-value $\leq$ 0.05) were included in this analysis (62 of 70 trees total); trees that did not produce robust S-map forecasts lacked reliable classifications. We used MAE in the randomization test to classify dynamics, but the overall fit of the model was measured by the significance of ρ_{max}. First, we tested for a difference between regions (Boston versus Ouachita Mountains) by including *region* as a control variable (both independently and as

an interaction with *health class*). Finding no regional difference ($p > 0.05$), we dropped the *region* term in subsequent regression model runs. We tested two versions of the regression model: maintaining three separate health classes (healthy, declining, and dying) and combining poor health classes for a total of two classes (healthy, and declining or dying). Results were robust to either specification, and we focus here on the latter for simplicity. We also tested the sensitivity of excluding the 8 trees that lacked reliable classifications from the regression; whether we included them or not, results were qualitatively similar.

RESULTS

In contrast with our hypothesis, nonlinear forecasting models revealed that healthy trees were significantly more likely to exhibit nonlinear dynamics relative to declining or dying trees (logistic regression, $p = 0.015$; Fig. 3). Declining or dying trees were one-fourth as likely to have nonlinear dynamics as healthy trees (odds-ratio on the coefficient for health class = 0.25). The majority (66%) of healthy trees from the Boston Mountains exhibited nonlinear dynamics. In the Ouachita Mountains, 11% of declining and 15% of dying trees exhibited nonlinear dynamics, compared to 46% of healthy trees in that region (Table 1).

DISCUSSION

Forecasting models highlight the nonlinear nature of many systems for which we can obtain time-series data, in a multitude of disciplines (Sugihara et al. 1996, Schittenkopf 2000, Hsieh et al. 2005, Glaser et al. 2014). Applied here, they reveal their utility for working with tree-ring data to assess forest responses to disturbance events. Specifically, they highlight how nonlinear growth dynamics of trees can be associated with survival during a disturbance, while linear growth dynamics appear linked to mortality. Univariate forecast models do not reveal the mechanisms at work driving these contrasting growth dynamics (see Sugihara et al. 2012 for multivariate extensions that can test environmental drivers). However, detection of nonlinear dynamics in individuals surviving disturbance

Table 1. Results of nonlinear forecast modeling for tree ring growth series from the Boston Mountain (17 trees) and Ouachita Mountain (45 trees) regions. Health class is defined in the text; we present results for declining and dying trees as a merged category ("Decl. + dying"), as well as separately. Dynamics were classified as linear or nonlinear by S-map models; percent (%) nonlinear shows the proportion of each health class exhibiting nonlinear dynamics. Series length represents the number of forecasts made by the model, related to the length of the time series and dimensionality. E, dimensionality (determined by simplex projection), is presented because of its importance for generating S-map output. ρ_{max} is the maximum Pearson correlation coefficient (or forecast skill) for the best S-map model of each series. Standard errors ($\pm$) are shown for each metric averaged over health class and dynamic classification.

				Linear growth patterns			Nonlinear growth patterns		
Region	Health class	n	% non-linear	Series length	E	ρ_{max}	Series length	E	ρ_{max}
Boston Mtns.	Healthy	5	80	89 ± 0	2.0 ± 0.0	0.31 ± 0.0	74 ± 2	3.5 ± 0.6	0.36 ± 0.0
	Decl.+ Dying	12	33	75 ± 4	4.5 ± 1.0	0.31 ± 0.0	75 ± 1	3.5 ± 0.6	0.40 ± 0.1
	Decl.	7	29	75 ± 4	3.8 ± 1.1	0.32 ± 0.0	76 ± 3	4.0 ± 1.0	0.37 ± 0.1
	Dying	5	40	75 ± 4	5.7 ± 2.3	0.27 ± 0.0	73.5 ± 1	3.0 ± 1.0	0.43 ± 0.1
Ouachita Mtns.	Healthy	24	46	65 ± 4	5.0 ± 0.7	0.57 ± 0.0	60 ± 4	4.7 ± 0.5	0.64 ± 0.0
	Decl.+ Dying	21	14	57 ± 4	3.6 ± 0.3	0.57 ± 0.0	64 ± 4	2.3 ± 0.7	0.62 ± 0.0
	Decl.	8	13	58 ± 5	2.9 ± 0.3	0.57 ± 0.0	70 ± 0	1.0 ± 0.0	0.65 ± 0.0
	Dying	13	15	57 ± 6	4.0 ± 0.4	0.57 ± 0.0	62 ± 5	3.0 ± 0.0	0.61 ± 0.0

events can serve as an important guide for investigators attempting to understand the costs and benefits of nonlinear dynamics in different systems. Specific to forests, we can use this tool to assess tree strategies for long-term survival. More fundamentally, we can begin to develop a means of addressing a deceptively simple question for which we currently have few answers: why do some trees die following disturbance when nearby, well-interspersed conspecifics appear to flourish? Fully addressing this question is beyond the scope of any individual project, but the current study offers a way forward by indicating that different growth strategies adopted by neighboring conspecifics may confer different capacities to respond to external disturbance.

Our results contradict our initial hypothesis: we found that healthy trees surviving this disturbance were significantly more likely to have nonlinear dynamics than trees that succumbed to mortality following the disturbance. Previous work on the same trees (Haavik et al. 2011) showed those with slower growth rates early in life were more likely to survive disturbance; we add to the understanding of this system by demonstrating these same resilient trees also displayed nonlinear dynamics in growth. While these findings contradict studies of populations under external stress that guided our initial hypothesis (Berryman 1991, Mullon et

al. 2005, Anderson et al. 2008, Glaser et al. 2014), it corroborates other work linking nonlinear dynamics to healthy individuals (Sugihara et al. 1996). In that study, human infants experiencing stress exhibited heart rhythms with underlying linear dynamics compared to their healthier counterparts (Sugihara et al. 1996). Our findings appear consistent with this work and suggest nonlinear dynamics can be linked to an increased ability to adapt to variable conditions, while linear dynamics may represent decreased adaptive coping abilities. Indeed, inter-individual differences in resource allocation strategies may cause inter-individual differences in senescence (Benton et al. 2006). The explanation for these apparently contradictory findings may lie in the scale of observation: studies that show stress is associated with nonlinear dynamics have been conducted at the population level, while studies reporting an association between stress and linear dynamics have been conducted on individuals. Our study falls into and corroborates the latter scale of observation. In so doing, our work highlights how "demographic performance heterogeneities" (Benton et al. 2006) among individuals within a population can have not just important, dynamical consequences for a population (Benton et al. 2006), but for individuals comprising the population as well.

Our approach to discerning different growth dynamics among surviving and dying trees has

several features important for research investigating forest resilience to disturbance. First, it can be employed at the level of the individual (Sugihara et al. 1996) or the population (Berryman 1991, Mullon et al. 2005, Anderson et al. 2008, Glaser et al. 2014). Second, it does not rely on the acquisition of ancillary environmental data. This is related to and expanded upon in our next point. Third, this approach does not require all individuals to be born at the same time (i.e., of the same cohort). When an investigator is analyzing dynamics of a set of organisms that might have been born at different times, the path-dependent nature of expressed traits such as mortality presents a challenge: an individual's response to a disturbance depends on both the current and past environments to which it has been exposed (Benton et al. 2006). When working with one cohort, these past and current environmental effects are essentially controlled. However, when the sample population is composed of individuals who represent multiple cohorts (perhaps dozens or hundreds of cohorts in the case of a forest of long-lived trees), controlling for both current and past environmental exposure is nearly impossible without a concurrent set of ancillary environmental data. Such datasets are, unfortunately, rare.

In spite of the advantages of using nonlinear forecasting models, the approach does not permit us to explore fully the mechanisms governing individual mortality or survival of trees with no obvious differences in microsite habitat, canopy status, or other features that might drive differences in resource availability. There are multiple mechanisms that could have driven the observed results. First, environmental forcing may be linear, but integrated in a nonlinear fashion by healthy trees (Hsieh et al. 2005, Hsieh and Ohman 2006). Second, and conversely, environmental forcings may express nonlinear dynamics but be integrated by dying trees in a linear fashion (Greenman and Benton 2003). Third, nonlinear dynamics in growth rings may be a manifestation of intricate and poorly defined interactions between environmental variables (e.g., temperature may drive growth only in the presence of sufficient moisture availability). Fourth, nonlinear dynamics may be driven by patterns of suppression and release amongst competing individual trees. Fifth, nonlinear dynamics may be driven by processes that require substantial C allocation not captured by radial growth indices such as tree C investment in masting, roots, foliage, or branches. Though any combination of these potential features could represent a possible means of generating nonlinear growth dynamics, it remains unclear why any such phenomena would influence healthy vs. dying trees differently.

Given that tree growth dynamics are the net result of a tree's ability to capture multiple resources, it is feasible that nonlinear growth dynamics were associated with surviving trees to a greater extent than with dying trees because these two growth strategies reflect differences in trees' abilities to capitalize on stochastic resource pulses. The nonlinear growth dynamics identified in this study may reflect a more nimble response by healthy trees to environmental cues which, in turn, may confer varying competitive advantages during changes in resource availability. Such phenomena are known drivers of differential survival in plants (Sher et al. 2004). Indeed, links between leaf nitrogen (N) concentrations and carbon accrual of healthy trees in this population (A. S. Boone and S. A. Billings, *in review*) suggest that capturing pulses of soil N may be important for growth responses of these oak trees and, more broadly, an important part of the N budget for N-limited vegetation (Gebauer et al. 2002). This seems feasible, given the generally N-limited nature of forests such as these (Nadelhoffer et al. 1999). Other studies emphasize the importance of light availability as a regulator of established oaks' growth; enhanced availability of light can result in sufficiently enhanced productivity of established oaks to prompt forest managers to reduce stand basal area by up to 40% to promote growth of the remaining oaks (Loftis 1990). Trees adhering to invariant growth strategies, observed as underlying linear growth dynamics, may have less capacity to capitalize on pulses of resources such as N, light or other necessary resources, perhaps ultimately resulting in increased vulnerability to mortality.

This work highlights several features of these trees' growth patterns important for beginning to understand why some trees survive disturbance while other conspecifics do not, as well as for the broader community of ecologists using dendro-

chronology as a tool. First, healthy trees' growth dynamics differed relative to dying and declining trees over a time series spanning their full lifespan, not just immediately before the disturbance. Our analyses thus imply that nonlinear growth dynamics throughout a tree's life can incur an advantage during forest disturbances. Thus, growth dynamics established well prior to the disturbance were a predictor of eventual mortality. The research that inspired this work demonstrated that healthy trees in both the Boston and Ouachita Mountains tended to grow more slowly early in their lives relative to trees succumbing to disturbance, though not to the extent that tree canopy class or bole diameter was evidently affected (Haavik et al. 2011). The current study expands on this knowledge by highlighting the apparent importance of nonlinear dynamics in some systems as a determinant of susceptibility to disturbance. Given that these patterns appear established early in a tree's life, their discovery well before a mortality-inducing disturbance could result in enhanced ability to predict tree susceptibility. Though we do not understand the mechanisms behind the observed pattern, its existence in these forests as well as in other, unrelated systems (Sugihara 1994, Mullon et al. 2005, Anderson et al. 2008, Vandermeer and Lin 2008, Glaser et al. 2011) suggests the importance of exploring the evolutionary advantages of nonlinear growth dynamics across taxa. This research goal is particularly pressing given predictions of increasing numbers and intensity of disturbance events in the coming decades.

Next, our work highlights an underappreciated feature of tree radial growth relevant for the dendrochronology community. Our observation of nonlinearity in tree growth dynamics is interesting given the widely-invoked assumption in many dendrochronological studies of stationary responses of tree growth to environmental conditions (Fritts 1976, Johnson et al. 1988, Graumlich 1991, Orwig and Abrams 1997). The presence of nonlinear dynamics in forest ecosystems may be a result of non-additive interactions between driving variables (Dixon et al. 1999), mis-matches between the time scale of environmental forcing and life history traits like generation time (Hsieh and Ohman 2006), or biological assimilation of low-frequency environmental variability (Greenman and Benton 2003). These

phenomena, if indeed they are at play in forested systems, highlight the difficulties of assuming a constant relationship between environmental forcing and tree growth responses. Even when correlations between tree growth and a particular environmental variable can be found, tree-ring growth and environmental forcing may correlate only over a well-defined, finite time period. Over longer periods, such correlations in nonlinear systems usually break down (Sugihara et al. 2012). These so-called 'mirage correlations' could create a problem for climate-growth reconstructions; nonlinear dynamics may result in variable growth responses to environmental forcing, resulting in tree-ring chronologies that do not accurately reflect environmental variation. Such a phenomenon may help generate the sometimes large proportion of growth variation left unexplained by environmental drivers.

Lastly, we highlight the utility of applying forecast modeling to time-series data already well-developed by the dendrochronology community. There is an ever-greater need for forecasting models to assist with sustainable ecosystem management, species abundance forecasts, and predictions of ecosystem boundary shifts given increased uncertainties about future ecosystem functioning. This approach appears particularly useful for tree-ring studies, which reveal integrated tree responses to a varying environment and often are characterized by lengthy time series. Applying these models to tree-ring time series thus represents an important way forward for understanding forest responses to environmental forcings.

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