



Analyzing the complexity of cone production in longleaf pine by multiscale entropy

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ABSTRACT

The longleaf pine (*Pinus palustris* Mill.) forests are important ecosystems in the southeastern USA because of their ecological and economic value. Since European settlement, longleaf pine ecosystems have dramatically declined in extent, to the degree that they are now listed as endangered ecosystems. Its sporadic seed production, which limits the frequency of natural regeneration, is identified as a significant factor in this decline. Previous studies did not characterize the complexity in cone production. Here a method of multiscale entropy is used to analyze long-term data for cone production in longleaf pine forests at six sites across its native range. Our results indicate that there exists a regime shift for cone production at each site. The corresponding time scales of the regime shift are generally 1–9, 10–12, 13–16, and 17–24 yr. Overall patterns for the complexity of cone production with the change of time scale are similar among sites, with exception of the Red Hills (FL). There are high correlations between entropy of cone production and entropy of annual mean air temperature and annual total precipitation at all sites. These results provide new insight into the complexity of cone production of longleaf pine forests with significant management implications.

KEYWORDS

Climate; management; regime shift; restoration

Introduction

Longleaf pine (*Pinus palustris* Mill.) forests are among the most important ecosystems in the southeastern United States because of their economic (e.g., quality timber and related forest products) and ecological value (e.g., high biodiversity and habitat for numerous plants and animals, including endangered and threatened species; Brockway, Outcalt, Tomczak, & Johnson, 2005; Hodges, 2006; Jose, Jokela, & Miller, 2006). These ecosystems once occupied a variety of habitats from xeric sandhills to poorly drained flatwoods to montane areas. They covered an estimated 33–37 million ha, distributed across a broad area from southeastern Virginia to eastern Texas, of which 23 million ha were dominated by longleaf pine and 14 million were mixtures with other tree species (Frost, 1993; Vance, 1895). The extent of longleaf pine ecosystems has dramatically declined since European settlement. By 1995, only about 1.02 million ha of longleaf pine forests remained based on

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forest inventory and analysis data (Outcalt & Sheffield, 1996). Longleaf pine ecosystems are therefore listed as critically endangered (Noss, LaRoe, & Scott, 1995).

One major factor contributing to the decline of longleaf pine is its intrinsic characteristics of sporadic seed production, which limits longleaf pine regeneration, impairs restoration efforts, and complicates management (Brockway, Outcalt, & Boyer, 2006; Frost, 2006). The physiological development of longleaf pine seed from initial primordia to conelet, through green cone to mature seed is a lengthy process, which can extend through a period of nearly 3 yr. A process of such long duration (and the many factors and events that may adversely impact cone and seed development during this extended period) may be a contributing reason as to why longleaf pine produces infrequent good seed crops. If an existing generation of this species cannot produce sufficient cones and seeds, then the local population will face extinction and entire ecosystems will be degraded.

The major stages of the reproductive process include development of male and female strobili, pollination of conelets, fertilization in the ovary, cone maturation, and seed production. Monitoring cone production on mature longleaf pine trees first began in 1958, at the Escambia Experimental Forest in Escambia County, Alabama. Since then, numerous other sites have been added to this range-wide effort, spanning the Southern Coastal Plain from Louisiana to North Carolina. Through intensive field observations (such as at the Escambia Experimental Forest), improved knowledge about the processes of cone production, relevant timelines, and influencing factors was obtained. Male strobili (catkins) predominate in the lower part of tree crown, while the female strobili (conelets) occur mainly in the upper part of crown (Schopmeyer, 1974). Catkins initiate in July, while conelets first form in August (Boyer, 1990). Female buds appear in mid-November and early December and male catkins develop between late December and early February (Boyer, 1981). Conelets appear in January or February. Boyer (1990) reported that the growth of catkins and conelets are almost entirely dependent on ambient temperature. Catkin production is favored by rainfall during the growing season, while conelet production is favored by a wet spring and early summer, followed by a dry period in late summer (Shoulders, 1967). Because of this differential in favorable conditions for each sex, conelet losses can be extensive, with frequently less than half surviving to maturity (e.g., Boyer, 1974; McLemore, 1977). Pollination occurs in late winter or early spring, but fertilization does not occur until spring of the following year. Conelets grow quickly after fertilization, becoming green cones, and reach maturity, as brown cones, between mid-September and mid-October of their 2nd yr (Boyer, 1990).

Although the exact mechanisms which cause such variation in cone production are still not known, it is very likely that the causative factors are rooted in the reproductive pattern derived from the 3-yr developmental cycle. The regular method is to correlate cone production per year with monthly precipitation and average temperature at local and regional scales (Pederson, Kush, & Meldahl, 1998; Pederson, Kush, Meldahl, & Boyer, 1999). The main findings to date from the Escambia Experimental Forest suggested that there are no strong relationships between temperature, precipitation, and cone production during the seeding year (Brockway et al., 2006; Pederson et al., 1998, 1999). Cone production is determined before final year of seeding and precipitation explains 48.6% of annual cone crop variation while average monthly temperature explains 33.7% (Pederson et al., 1998, 1999). After comparing cone production and local climate

(temperature and precipitation) at 10 sites across the southeastern region, Guo, Stanley, Chen, and Brockway (2016) indicated that the relationship between cone production and climate is complicated, such as the frequency of high cone production did not match the frequency of high annual precipitation.

Trees with highly variable seed production during their life spans are called mast seeding trees. This trait is fairly common among tree species and is characteristic of longleaf pine. Previous studies of mast seeding tree species reported that resource supply and environmental conditions are obviously involved in reproduction, but the nature of this involvement is still incompletely understood (Kelly & Sork, 2002). The resource-matching hypothesis stipulates that the reproductive effort of trees is strongly dependent on climate conditions, such as air temperature and precipitation (Kelly, 1994; Koenig & Knops, 2005). Others contend that mast seeding is an evolved reproduction strategy (Janzen, 1971; Norton & Kelly, 1988). If mast seeding is dependent on climate, then, it is reasonable to assume that patterns of cone production should correspond to patterns of local climate, which means the dynamics of cone production for longleaf pine at different locations (or local climate) should be quite different. Otherwise, if cone production behaviors are similar at different sites, then, it means an evolved reproduction strategy. However, there has so far been only limited study of the complexity in patterns of cone production for longleaf pine.

Entropy, usually related to order and predictability, is used to characterize complexity in physics and ecology (e.g., Chen, Li, & Collins, 2005; Costa, Goldberger, & Peng, 2002). Here we apply a method of multiscale entropy to characterize and compare the complexity patterns of cone production in longleaf pine, based on available long-term monitoring data. Our specific objectives include (a) characterizing complexity patterns of cone production in longleaf pine among different sites; (b) evaluating whether longleaf pine forests at different sites follow the same complexity patterns in cone production; and (c) exploring the relationships between complexity of cone production and local patterns of climate.

Materials and methods

Data collection

Cone production data for longleaf pine were collected as part of a long-term monitoring effort conducted by research scientists at the Southern Research Station of the U.S. Department of Agriculture Forest Service. Observers used 8–10× binoculars each spring at numerous sites across the southeastern region to count the number of green cones and unfertilized conelets present in the crowns of mature longleaf pine trees growing in low-density stands. At least 10 trees were sampled in stands at each site. The mean number of cones on all sampled trees was used to represent the average for each site. Detailed information can be found in Brockway (2015). In our study, six sites with the most complete data were selected from the regional monitoring effort. These six sites include the (a) Escambia Experimental Forest in southern Alabama, (b) Red Hills of northern Florida, (c) Blackwater River State Forest in the western panhandle of Florida, (d) Jones Center in southwestern Georgia, (e) Sandhills State Forest in northeastern South Carolina, and (f) Kisatchie National Forest in Louisiana. Climate data, including annual mean air temperature and total precipitation, were acquired from weather stations near each monitoring site.

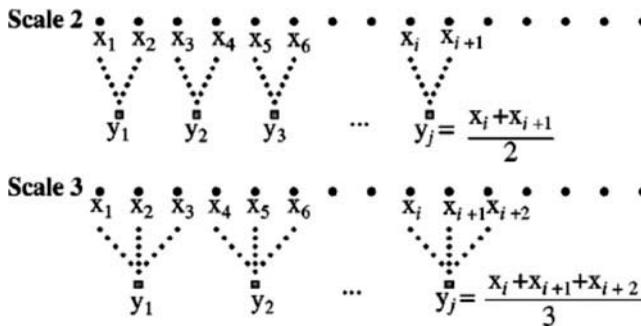
Methods

Multiscale entropy, which was first proposed by Costa et al. (2002), is a method for analyzing the complexity of nonlinear and nonstationary signals in finite length time series. It consists of two main procedures—namely, graining (scale) and calculation of entropy for each grained time. In our study, entropy is defined as the Shannon entropy $H_\epsilon(x)$ of cone production (or air temperature and precipitation) at different time scales of ϵ (length of years) as the following:

$$H_\epsilon(x) = \sum p_\epsilon(x) \text{LOG}_{10} p_\epsilon(x), \tag{1}$$

where $p_\epsilon(x)$ is the probability (percentage) of cone production (x) at the i th year measured using samples of ϵ units in size (see the diagram below). The time scale of ϵ includes 1, 2 ... $m/2$ or $(m - 1)/2$. The percentage is calculated as:

$$p_\epsilon(y) = \frac{y_i}{\sum y_i} \times 100, \tag{2}$$



Here $H_\epsilon(x)$ describes the temporal distribution of cone production along the temporal length scale ϵ . Higher values of $H_\epsilon(x)$ represent higher temporal evenness of the cone production at time scale of ϵ years.

The fractal dimension (D_I) is used to measure the complexity or the change of H_ϵ at different scales (1, 2 ... $m/2$ or $(m - 1)/2$ along the time series (m year), and it is estimated by:

$$D_I = \lim \frac{H_\epsilon}{\text{LOG}_{10}(1/\epsilon)}. \tag{3}$$

A similar method was used to characterize the patterns of two grass species at the Sevilleta Long-term Ecological Research area (Chen et al., 2005). More detailed information can be found in Costa et al. (2002) and Chen et al. (2005).

The Spearman correlation between the multiscale entropy of cone production and climate variables (e.g., annual temperature and total precipitation) was conducted by SAS software (Version 9.3, SAS Institute Inc., Cary, NC, USA). Statistical significance was discerned at $p < 0.05$.

Results

A general trend of increased entropy with expanding time scale was found at each site, which means cone production becomes more even at each site as the time scale increases (Figure 1). While four domains of scale—referring to a region where entropy pattern remains the same or changes linearly, in the entropy of cone production—occur at most sites, there are only two domains at the Red Hills site (Table 1). This indicates that there was a regime shift of cone production for longleaf pine in stands at each site, which means different stable states for cone production, such as from the domain of 9 to 3 yr here. The four domains approximately correspond to the time scales of 1–9, 10–12, 13–16, and 17–24 yr. Although there are differences in the slopes of fitted lines (D_i) and the extent (length of years) of domain among the five sites (Escambia, Blackwater River, Sandhills, Jones Center, and Kisatchie), the overall patterns of complexity in cone production with

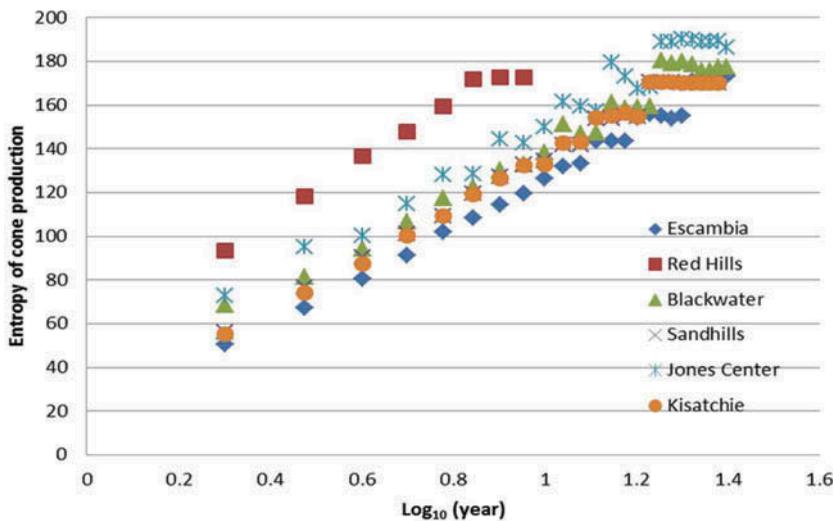


Figure 1. Change of entropy for cone production in longleaf pine forests at different sites across the southeastern United States.

Table 1. Comparing the complexity of longleaf pine cone production among study sites across its native range.

	Escambia Experimental Forest (Alabama)	Red Hills Florida (Florida)	Blackwater River State Forest (Florida)	Jones Center (Georgia)	Sandhills State Forest (South Carolina)	Kisatchie National Forest (Louisiana)
Observation years	57 (1958–2014)	16 (1999– 2014)	48 (1967–2014)	48 (1967– 2014)	46 (1969–2014)	46 (1967–1974, 1977–2014)
Domain number	4	2	4	4	4	4
Time scales for domain (years)	1–11, 12–14, 15–19, 20–24	1–5, 6–8	1–9, 10–12, 13–16, 17–24	1–9, 10–12, 13–16, 17–24	1–9, 10–11, 12–15, 16–23	1–9, 10–11, 12–15, 16–23
Slope of fitting line with R^2 and p	115.38 $R^2 = .9916$ $p < .01$	128.46 $R^2 = .9827$ $p < .01$	108.51 $R^2 = .9782$ $p < .01$	112.42 $R^2 = .9734$ $p < .01$	111.41 $R^2 = .9864$ $p < .01$	113.66 $R^2 = .9857$ $p < .01$

the change of time scale are similar. The slopes of fitted lines are concentrated around 111–115. Only the Red Hills site deviates from this pattern.

At each site, there is a high correlation between the entropy of cone production and entropy of annual mean air temperature and annual total precipitation, respectively (Figure 2). This means that the complexity of cone production for longleaf pine is correlated with local climate variables (i.e., annual air temperature and precipitation).

Discussion

Complexity and regime shift

Previous studies of cone production for longleaf pine and other mast seeding trees focused on the detailed biological or ecological factors, which may contribute to the fluctuations in cone production. Our study discovers the pattern of complexity in the dynamics of cone production at different sites. The complexity of cone production for longleaf pine stands at different sites can be quantitatively evaluated by the multiscale entropy method. Our results indicate that regime shift in cone production with different time scales occurred at each study site, during the observational time period of the longleaf pine stands.

Regime shift indicates that a system has a directional change and change to a new temporary or permanent equilibrium state (Carpenter & Cottingham, 1997; Easterling & Peterson, 1995). The domains of scale refer to the regions of the spectrum for a specific

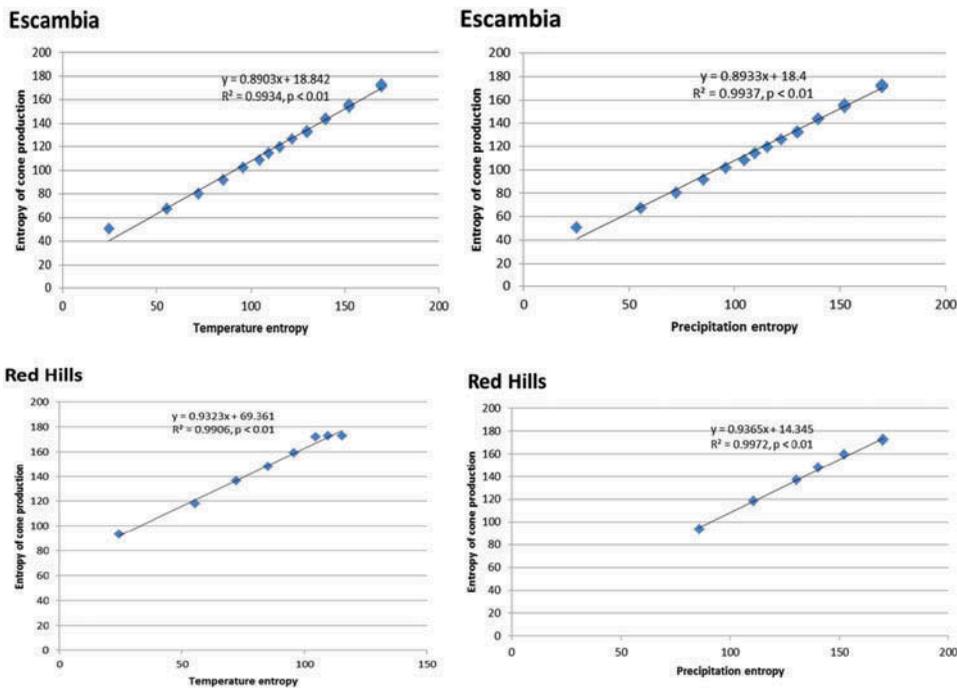
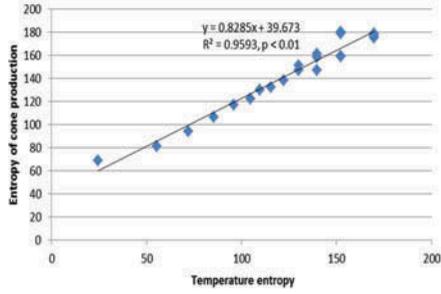
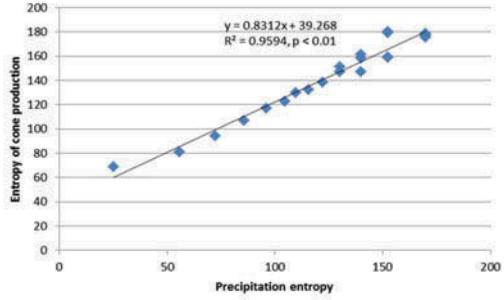


Figure 2. Relationships between entropy of cone production in longleaf pine forests and entropy of annual mean air temperature and annual total precipitation, respectively.

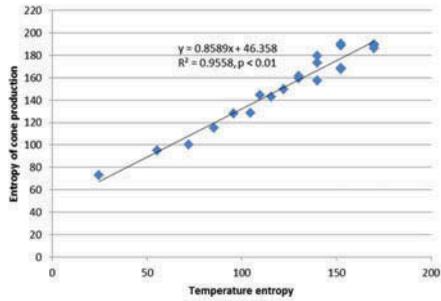
Blackwaters



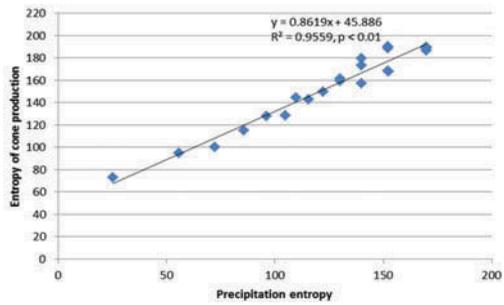
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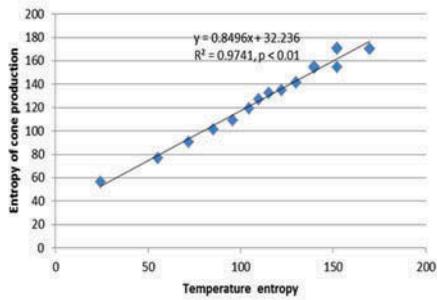
Jones Center



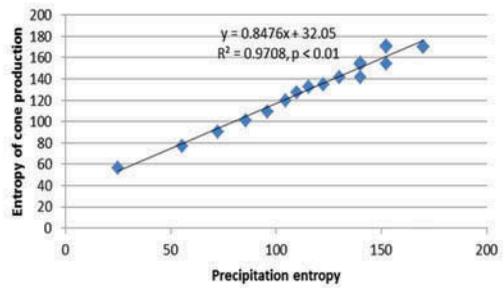
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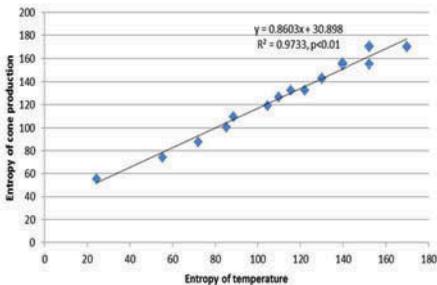
Sandhills



Sandhills



Kisatchie



Kisatchie

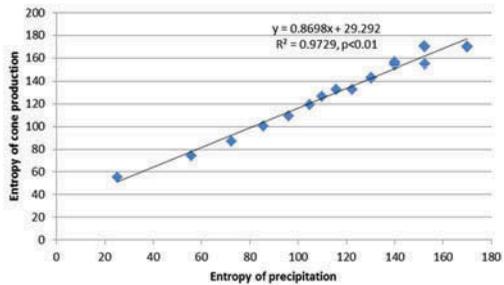


Figure 2. Continued.

ecological process where patterns do not change or change monotonically with the change in scale (Wien, 1989). Domains can be separated by relatively sharp or slow transition areas. One regime may be composed of one to several domains. The corresponding time scales for regime shift in cone production vary among sites. But with current data, they are approximately 1–9, 10–12, 13–16, and 17–24 yr at five sites, except for the Red Hills. The exception of Red Hills may be due to (a) a relatively short time period for observation (1999–2014); (b) potential difference in genetic composition; and (c) contribution from other factors (e.g., soil and fire).

The similar behavior among different sites may indicate that complexity of cone production is an intrinsic character of longleaf pine. These different time scales may help explain the sporadic cone production of longleaf pine. Such information may also provide useful clues for predicting cone production, perhaps contributing to model development in the future. The regime shifts at different spatial and temporary scales should be incorporated into cone production models. Previous studies of fluctuations in cone production yielded contradictory findings or inconsistent patterns, because the multiple time scales inherent in such time series and the regime shift in cone production were not considered. Guo et al. (2016) highlighted the value of long-term data for such studies, noting that results based on short-term observations can be misleading and, at best, inconsistent when comparing different locations.

Climate factors

The high correlation between entropy of cone production and local annual air temperature and total precipitation at all sites may indicate (a) a constraint of local climate on cone production; and (b) other environmental factors may be unimportant. Although weather in some years may cause fluctuations in the cone production, the climate still has an important limitation on cone production on a multiyear scale. Our results seem to also support the resource-matching hypothesis, which indicates that the reproductive effort of trees is strongly dependent on climate conditions, such as air temperature and precipitation (Kelly, 1994; Koenig & Knops, 2005), but in a complicated way. Since the complexity of cone production is different among different sites, but exhibits similar patterns across differing sites, perhaps mast seeding in longleaf pine is an evolved (or coevolved) reproduction strategy (Janzen, 1971; Norton & Kelly, 1988). These hypotheses may coexist here.

Our results indicate that past climate fluctuations did not affect the general correlation between the entropy of cone production and climate among different sites. Given the high correlation between the entropy of cone production and entropy of temperature and precipitation, the currently changing global climate may affect cone production in longleaf pine. However, whether this type of correlated relationship would still exist under increasingly more rapid rates of change is an unanswered question. Although it is not clear which mechanisms could cause the observed regime shift in cone production, efforts to incorporate this complexity in the cone prediction aspect of climate-driven scenarios need to include climate effects at suitable time scales. Simple scaling from one level of scale to another scale, when modeling cone production in longleaf pine forests, may risk imprecision at best and erroneous estimates otherwise.

Management implications

Individuals engaged in restoration and management of longleaf pine ecosystems will benefit from recognizing that longleaf pine cone production is a varied process. The timing of regime shifts (such as 9, 3, 3, and 7 yr in this study) may indicate periods of higher cone production and practitioners will be well advised to plan management actions accordingly. For example, to increase longleaf pine seedling germination, survival, and establishment, forest land managers may use prescribed fire in a manner that prepares a favorable seedbed, in the weeks prior to seed fall during a high production year. Prescribed burning should then be avoided during the following year or two, to minimize seedling mortality from fire. Managers may also wish to limit seedling mortality, during this establishment phase, by excluding domestic livestock from the site and controlling populations of wild hogs (*Sus scrofa*), which pullup and consume the high-starch taproots of longleaf pine seedlings.

Here we used historical time-series data of cone production and discovered that regime shifts occurred. Forest managers (or decision makers) would benefit by having foreknowledge about the timing of regime shifts. Thus, further study is needed to precisely determine in advance the timing of regime shifts for longleaf pine cone production.

Conclusion

Ecological systems and their biological components are widely understood to be regulated by interacting mechanisms, which operate across multiple spatial and temporal scales. The output variables of these systems often exhibit complex fluctuations that are not simply due to noise, but rather contain information about the underlying dynamics (Costa et al., 2002). The observed patterns may be understood as emerging from a collective behavior of different spatial and temporal scales (Levin, 1992).

Description of the complexity across different time scales and sites may improve our understanding of ecosystem dynamics in response to climate variables, by helping with the development of simplification, aggregation, and scaling for cone production in longleaf pine. Based on long-term data from longleaf pine forests at five sites in the southeastern United States, we found that complexity exists in cone production across different time scales. Furthermore, the complexity of cone production has a high correlation with the complexity of local climate variables, such as annual mean air temperature and total precipitation. Our findings, concerning the spatial and temporal dimensions of complexity in these ecosystems, provide new insights about the sporadic behavior of cone production in longleaf pine forests.

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