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NOTE

Critical slowing down in cone production of longleaf pine trees

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ABSTRACT
Longleaf pine forests were historically distributed throughout the southeastern United States and played an important role in local sectors of society, economy, and ecology. The longleaf pine became an endangered ecosystem due to over-harvesting, broad land-use change, and fire suppression. One major factor that has challenged restoration efforts is sporadic seed production. Based on collected cone production data in the past six decades, we tested whether critical slowing down existed in cone production at three longleaf pine locations. Our results indicated decreased variance and increased autocorrelation in variance before a high cone production. These results provide a new understanding of cone production from the perspective of a dynamic system. This method may be helpful in predicting years of favorable cone production for forest management.

KEYWORDS
Autocorrelation; extreme value; dynamic system; reproduction; variance

Introduction

Longleaf pine (*Pinus palustris* Mill.) forests are an important ecosystem from social, economic, and ecological perspectives across the southeastern United States. The forests provide economic sources from high-quality timber, pine straw, and related wood products (such as historical naval stores including turpentine, rosin, pitch, and tar), and the management of forests creates job opportunities for local societies. Longleaf pine forests also protect local watersheds and host high levels of biodiversity and endemic species, such as the red-cockaded woodpecker (*Picoides borealis*), gopher tortoise (*Gopherus polyphemus*), and black pine snake (*Pituophis melanoleucus*) (Jose et al. 2006). The area of longleaf pine forest ecosystems decreased from about 37 million hectares to 1.02 million hectares between the time of European settlement and the late 20th century due to factors such as over-harvesting, land-use change (agricultural development), and fire suppression. Currently, longleaf pine forests have been classified as endangered ecosystems. Another important factor leading to the decline of longleaf pine forests has been their sporadic seed production (Frost 2006), which affects longleaf pine regeneration and restoration due to the limited supply of seedlings. The insufficient seedling establishment results in losing forest sites to other species with more consistent annual patterns of seed production. Consequently, predicting good cone crops is critical for restoration planning.

Recent studies indicated the complicated relationships between climate factors (e.g., temperature and precipitation) and longleaf pine cone production (Chen et al. 2016; Guo et al. 2016). The tree species showed a weak burstiness in cone production and consistent information entropy (Chen et al. 2016, 2021). However, instances of

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prodigious cone production (bumper year, >100 cones/tree) have occasionally occurred at different sites throughout the southeastern region. These rare and extremely high cone production events have important implications for longleaf pine natural regeneration, seed collection for future artificial regeneration efforts, wildlife populations, and food chains. So far, there are limited studies on estimating the time of extremely high cone production (Chen et al. 2021).

Due to the severe consequences and potential applications, extreme events have gained significant recognition and have been studied from different perspectives, such as diseases, oceanography, climatology, sociology, finance, and ecology (e.g., McMichael 2015). Extreme events are considered the result of complex dynamical systems, and it is challenging to propose a precise and efficient strategy for prediction (Chowdhury et al. 2021). In ecological research, some ecosystems can change their status quite dramatically to an alternative state. Recent studies suggested that such critical transitions may be indicated in advance by generic indicators, and this phenomenon is known as critical slowing down (Scheffer 2009). Dakos et al. (2012) proposed variance and autocorrelation as indicators for critical slowing down, and their analytics and simulations indicated that variance sometimes might decrease, however, autocorrelation always increases to a critical transition. Thus, such changes may be used as early warning signals for underlying transition.

The temporal dynamics of longleaf pine cone production have shown some complex characteristics, such as power laws, burstiness, and spatial synchrony (Chen et al. 2018, 2021). This study aims to test whether there is a critical slowing down in the temporal dynamics of longleaf pine cone production. The detailed objectives include (i) whether the variance of cone production decreased, (ii) whether autocorrelation increased before the sudden increase of cone production, and (iii) whether there are detectable early signals. This study may provide a method to predict the possible high production year in cone production.

Materials and methods

Cone data and sites

Each spring, research scientists from the Southern Research Station of the USDA Forest Service used binoculars to count the number of green cones in the crowns of mature longleaf pine trees growing in low-density stands at several sites across the southeastern region. These cone production data of longleaf pine have been collected as part of long-term monitoring work.

On each site, at least ten fixed trees were monitored in stands. The average number of cones on all monitored trees was used to represent the cone production on each site. Detailed information is provided in Chen et al. (2016). In this study, three locations with continuous data were selected from the region. These three sites include the (1) Escambia Experimental Forest in southern Alabama from 1958 to 2021, (2) Blackwater River State Forest in the western panhandle of Florida from 1967 to 2021, and (3) Kisatchie National Forest in central Louisiana from 1977 to 2021.

Methods

The variation of cone production for the longleaf pine population at each site was calculated from the second available year to 2021. For example, at the Escambia site, cone production data were from 1958 to 2021. The variance was calculated each year from 1959 to 2021. In order to display variances and cone production dynamics in the same graph, here variance/10 was used. Autocorrelation was calculated between the cone production $N_1 \ldots N_t$ and $N_2 \ldots N_{t+1.}$ Correlation analysis was performed by using the least-squares technique by SAS software (Cary, NC). The statistical test was considered significant at $p < .05$.

Results and discussion

There were decreased (or stabilized) variances before the bumper year of cone production at each site (Figure 1). There were big jumps in variances when the cone production reached 100 or more cones per tree, followed by periods of gradually decreasing variances. A slight increase in variances could be observed when the cone production reached 40 cones per tree.

There was no significant autocorrelation in the cone production before any bumper year at the three sites, as shown by Figure 2 for one bumper event in each of the three sites. However, a significant autocorrelation existed in the variances of cone production before a bumper year. This relationship existed at the three sites for all bumper events, but is shown in Figure 3 only for one bumper event in each of the three sites(Figure 3). Usually, when the R^2 of autocorrelation in variances approached a 0.97 level, the next bumper cone crop might happen.

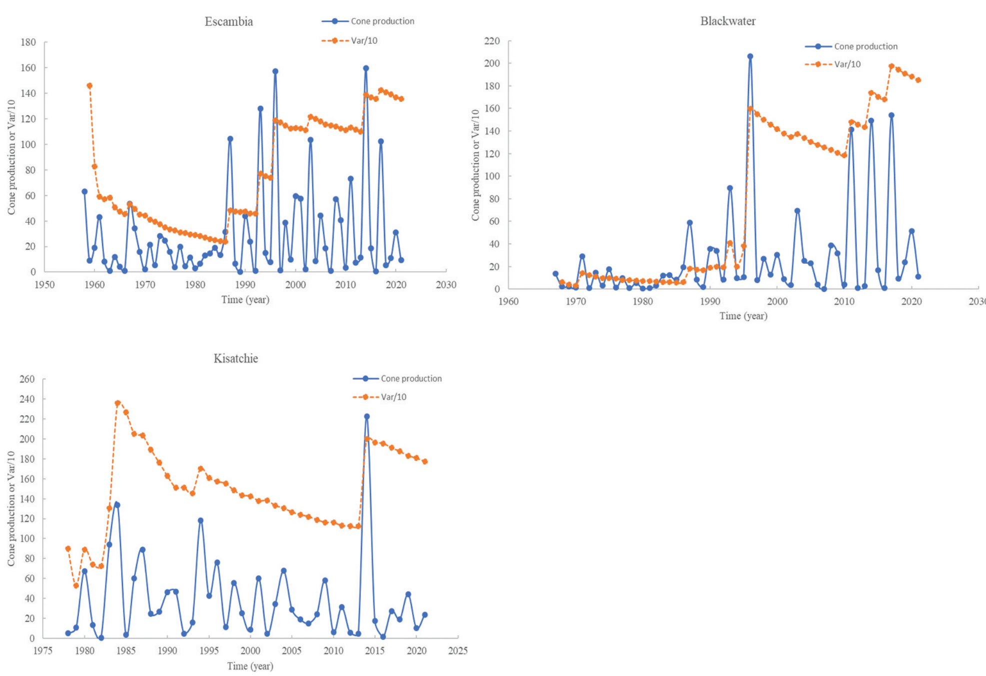

Figure 1. The dynamics of longleaf pine cone production and variance (variance/10) at three locations.

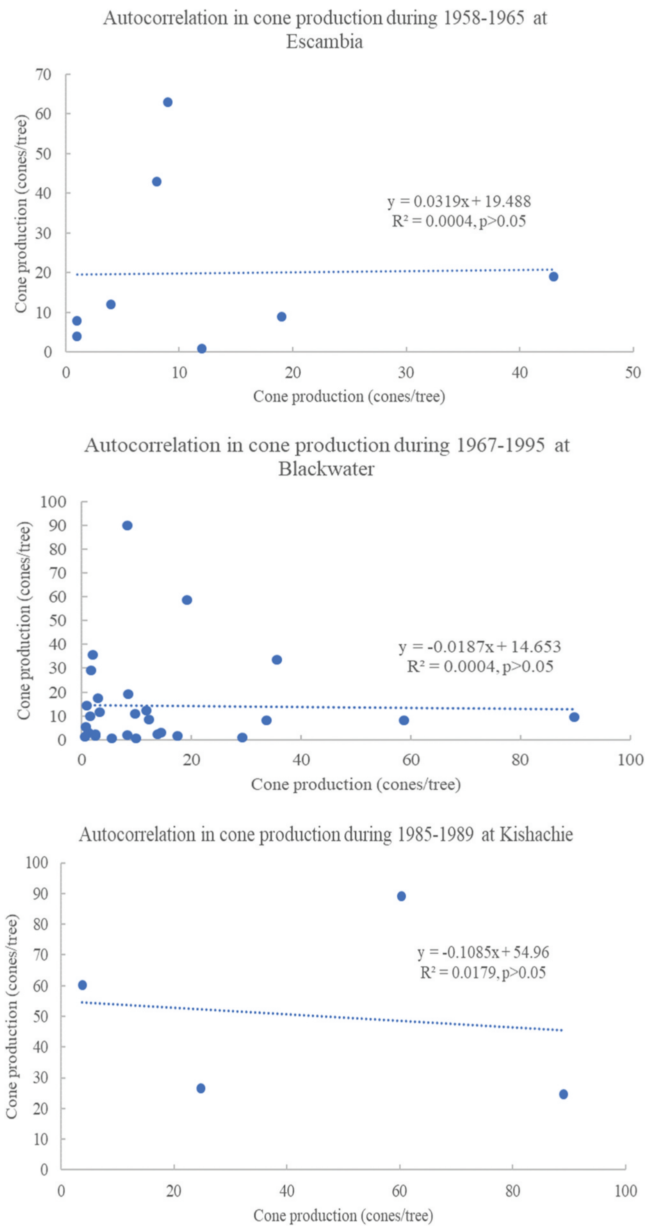

Figure 2. The autocorrelation of longleaf pine cone production at three locations.

This study found evidence that the phenomena of critical slowing down existed in the temporal dynamics of cone production in longleaf pine trees at different locations. The evidence included decreased variances and increased autocorrelation in variances.

The biological mechanisms of high cone production were complicated and related to external and internal interactions (Chen et al. 2021). Here we show that the variance of cone production increased dramatically when a high output of cones occurred. But after that, the

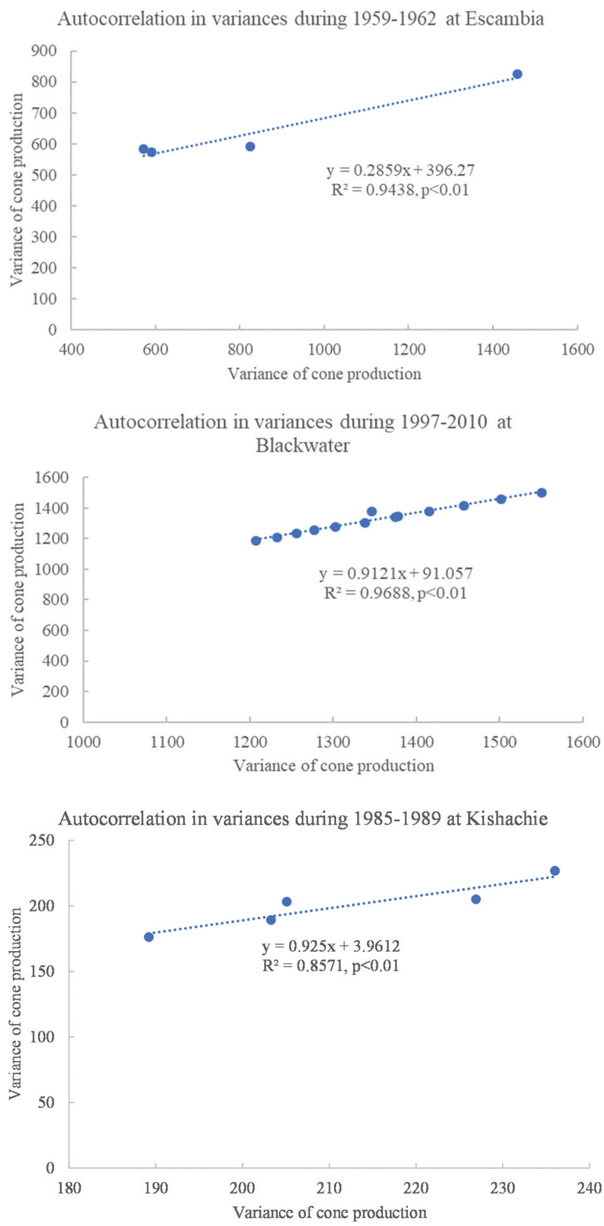

Figure 3. The autocorrelation in the variance of longleaf pine cone production at three locations.

variance of cone production started to decrease or stabilize before another high production. This phenomenon can occur when environmental factors fluctuate randomly, and the system becomes less sensitive to these factors when it approaches the threshold or when critical slowing down reduces the system's capacity to follow frequent environmental fluctuations (Dakos et al. 2012).

This simple approach makes it possible to estimate the next time of high cone production based solely on cone time series data. But in order to know the details, information on environmental fluctuations is needed. Based on the change in environmental factors, it may be practical to conduct a similar change through possible human activities to increase cone production.

As previous studies indicated, there was increased autocorrelation before an extreme value occurred (Scheffer 2009; Dakos et al. 2012). In this study, we did not observe the increase of autocorrelation in the annual cone production data before a high cone production happened. However, the rise of autocorrelation in the variance was observed. When the correlation coefficient (R^2) reaches a certain level (i.e., R^2 = 0.97), it may indicate that a bumper cone crop is likely to occur in the subsequent year.

Therefore, the variance of cone production can work as the early-warning signal of cone production in longleaf pine trees with limited data. The decreased (or stabilized) variance and increased autocorrelation in variance can indicate a high production in the next year, although the precise ecological mechanisms may still need to be discovered. This information will be helpful in forest management, such as seed harvesting for nurseries, forest regenerating, and hunting. Our results may bring a new understanding of cone production in longleaf pine from a complex system perspective.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Author contribution

XC: designing, testing, writing; KAB: confirming, editing; JLW: data providing, revising.

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