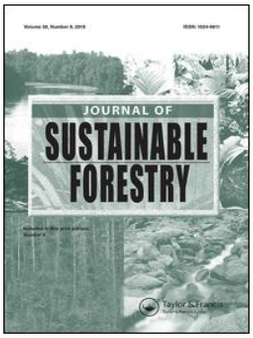

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Burstiness of Seed Production in Longleaf Pine and Chinese Torreya

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ABSTRACT

Different trees may have different seed production behaviors. Understanding the spatial and temporal patterns in seed production is important for sustainable forest management. A common feature in many complex systems is burstiness in their activity patterns. Burstiness is defined here as intermittent seed production. We studied burstiness in the seed (cone) production of longleaf pine (*Pinus palustris*) and Chinese Torreya (*Torreya grandis*) for the first time. Results indicated that burstiness characterized the seed production for both tree species. Burstiness ranged between low negative and low positive values and varied by species and locations. Generally, there existed scaling relationships between seed production and average inter-event years for both species, but the scaling exponents were different at locations. The average inter-event time was long for episodes of high seed production. These results suggest that complex seed production systems may be governed by some generic principles. Understanding burstiness in tree seed production may provide new knowledge about tree growth dynamics and their reproduction behaviors. This would be useful in sustainable forest management for estimating when the next high seed production episode is likely to occur and identifying sites with a short inter-event time for high seed production.

KEYWORDS

Average inter-event time; scaling relationship; seed production system; sustainable forest management; *Pinus palustris*; *Torreya grandis*

Introduction

The dynamics of complex systems are driven by the emergent activity from many loosely connected components, such as those in some ecosystems or individuals in a society. There is an increasing body of evidence supporting the existence of time-resolved activity in some systems, such as solar flares, airplanes' arrivals at hub airports, e-mail, web browsing, and gene expression patterns (Datlowe et al., 1974; Dezsö et al., 2006; Eckmann et al., 2004; Golding et al., 2005; Ito & Nishinari, 2015). A common feature across these complex systems is the presence of burstiness in each system's activity patterns. A burst means a high level of activity during a short period of time followed by a longer period of inactivity. Multiple repetition of this sequencing results in a longer-term pattern that reflects the process dynamics of the system under consideration. These observations suggest that the timing of many activities follows non-Poisson statistics, where they are characterized by bursts of rapidly occurring events, separated by longer periods of inactivity (Barabási, 2005). In human dynamics,

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burstiness, defined here as the intermittent for a given activity, has been reduced to a fat-tailed feature in the distribution of response time (e.g., e-mail). Burstiness can affect such things as resource allocation and the spreading of viruses, and deviations from burstiness in human heartbeat behavior may indicate illness (Thurner et al., 1998; Vazquez et al., 2007).

Seed production is an important regulator of stand regeneration and population dynamics for tree species, which determines the forest sustainability. Seed production, for some species with lengthy reproduction processes, often has complex relationships, which include intrinsic (e.g., genetics, life history) and extrinsic (e.g., climate, resource availability) factors (Campbell & Halama, 1993). For example, the intermittent and synchronous production of large seed crop is known as masting (Janzen, 1969; Kelly, 1994), which was defined as the synchronous production of seed at long intervals by a population of plants (Janzen, 1976). As a strategy, plants can also vary the length of endogenous cycles in seed production (Koenig et al., 1994; Sork et al., 1993). The masting concept emphasizes the spatial behavior of different populations, but it is not explicit to characterize temporal heterogeneity of population reproduction, especially for those not masting species which need multiple years to complete seed production. The cone production of longleaf pine (*Pinus palustris*) has been observed to be high during certain time periods, followed by a period of low production and then another episode of high production although longleaf pine is not a strong masting species (Chen et al., 2018). Recently, it was also found that the sporadic cone production of longleaf pine forests, at multiple sites across its range, followed power laws (e.g., frequent power law and Taylor's power law) (Chen et al., 2016a, 2017; Guo et al., 2016). So, it can be hypothesized that burstiness may exist in the time distribution of seed (cone) production for longleaf pine. For an economically important trees species with a complex reproductive process and such variable seed production, an important question for private landowners or/and public land managers to maintain forest sustainability is, "How long must they wait for the next episode of high seed production?"

The time intervals between the two contrasting events (e.g., high-high or low-low) have seldom been analyzed. Here we use long-term data for two unrelated tree species, longleaf pine, and Chinese Torreya (*Torreya grandis*), growing on different continents (North America and Asia, respectively) to study (i) whether burstiness characterizes in their seed (cone) production; (ii) whether there are patterns in the time interval between two events (inter-event) of high seed production; and (iii) whether there are similar patterns of burstiness or inter-event time in seed (cone) production at different locations for each species. This analysis is the first to use the concept of burstiness to characterize tree seed production. The pattern of time between two bursts of seed production may point toward a new perspective concerning this intrinsic property of each species and also help foresters to better understand the biological dynamics and anticipate the next episode of high seed production, which can be used for sustainable forest development.

Materials and methods

Data sets

Historically longleaf pine forests were among the most important ecosystems in the southeastern United States, because of their ecological and economic value (Brockway, Outcalt & Boyer, 2006). Since the 1950 s, cone production data for longleaf pine have been collected by scientists at the Southern Research Station of USDA Forest Service as part of a long-term region-wide monitoring study. After counting the number of green cones present in tree

crowns during the spring of each year, the mean number of green cones on all sampled trees was used to estimate the average production at each site. The detailed information can be found in Chen et al. (2016a, 2016b, 2017), Guo et al. (2017), and Guo et al. (2016). For this study, four sites with the most complete data were selected (Figure 1a). These four sites are (1) Escambia Experimental Forest in southern Alabama (short name Escambia), (2) Blackwater River State Forest in the western panhandle of Florida (Blackwater), (3) J.W. Jones Ecological Research Center in southwestern Georgia (Jones Center), and (4) Sandhills State Forest in northeastern South Carolina (Sandhills). The pollen data for longleaf pine were collected at the Escambia Experimental Forest by using pollen traps during the 1957–2013 period. Details about this technique are found in Guo et al. (2017).

Chinese Torreya is an economically important tree and a major source of income in local communities (Chen & Chen, 2019; Chen & Jin, 2019). This tree species is distributed across mountainous areas in southeastern China, particularly in Zhejiang, Anhui, and Fujian Provinces (Li & Dai, 2007). The two Torreya study sites are located at Zhaojiazhen in Zhuji City and the nearby Jidongzhen in Shaoxing City, both in Zhejiang Province of China (Figure 1b). These sites are within the major production area for this tree (Chen & Chen, 2019; Chen & Jin, 2019). Torreya seed yield information was obtained from the two local communities (Li & Dai, 2007).

Figure 1. Four study sites for longleaf pine in the southeastern USA (1: Escambia, AL; 2: Blackwater, FL; 3: Jones Center, GA; and 4: Sandhills, SC) (a) and two study sites for Chinese Torreya in Zhejiang Province of China (Zhaojiazhen and Jidongzhen) (b).

Burstiness

Burstiness (B) of the inter-event time of a certain seed production (x) was calculated as the following (Goh & Barabási, 2008):

$B_x = \frac{r-1}{r+1}$, where r is the standard deviation of inter-event year/mean of an inter-event year. B has the value of −1 for a regular time series as standard deviation is 0; B is 0 for random time series (or Poissonian) as r is 1; B approaches 1 for extremely bursty time series. In this study, x is seed (cone) production. Based on B value, time series of seed production can be classified. In thatwe do not know the threshold of seed production, various cone production levels (x), such as $x \geq 10, 20, 30, 40, 50 \ldots$and 100 (number of cones for longleaf pine and tons for Chinese Torreya) were used in the analysis. The inter-event time for different seed (cone) production (x) was counted from the time series and after that the average and standard deviation were calculated. The scaling relationship between seed production levels and average inter-event years was computed through regression analysis using SAS software (Cary, NC). The statistical significant level is set at $p < .05$.

Results

Burstiness changed with the cone production levels at each site (Figure 2). Most burstiness values were within −0.35 to 0.1. No higher burstiness levels were observed. Burstiness values were all negative at the Blackwater and Jones Center sites. With an increase of cone production thresholds, the average inter-event year increased at all sites (Figure 3). There was a significant correlation between cone production threshold and average inter-event year at each site ($p < .05$). The Jones Center site exhibited a smaller inter-event year for higher cone production.

Burstiness for Chinese Torreya also changed with the seed production thresholds (Figure 4a). At Zhaojiazhen, burstiness was between −0.4 and 0.2, being negative when seed production was less than 300 tons in the entire area. At Jidongzhen, burstiness was between −1 and 0.2 and positive only when seed production was approximately 100 tons. The average inter-event time was higher at Jidongzhen than at Zhaojiazhen (Figure 4b).

Discussion

The term, burst, is often considered to be a metaphor. In this study, the inter-event times of seed (cone) production were quantitatively analyzed by burstiness, because the timing for a burst is important to understanding forest dynamics and developing a sustainable management strategy. It is important to characterize the temporal dynamics of seed production (Chen et al., 2018). Doing so enhances the odds of regeneration success and decreases the risk of management failure. The inter-event times were not randomly distributed, following by Poisson processes. Rather, they displayed a remarkable heterogeneity in burstiness across the four sites for longleaf pine forests. This is consistent with the earlier work, showing changing recycle times (e.g., 3 years from a biological perspective) in the dynamics of cone production, when multiscale entropy and wavelet methods were applied (Chen et al., 2016a, 2016b; Guo et al., 2016).

Burstiness was also related to the given threshold of cone production. Escambia and Sandhill sites had a positive burstiness for cone production around 20–40 and 60–80 cones per tree, respectively. But Blackwater and Jones Center sites always had a negative burstiness,

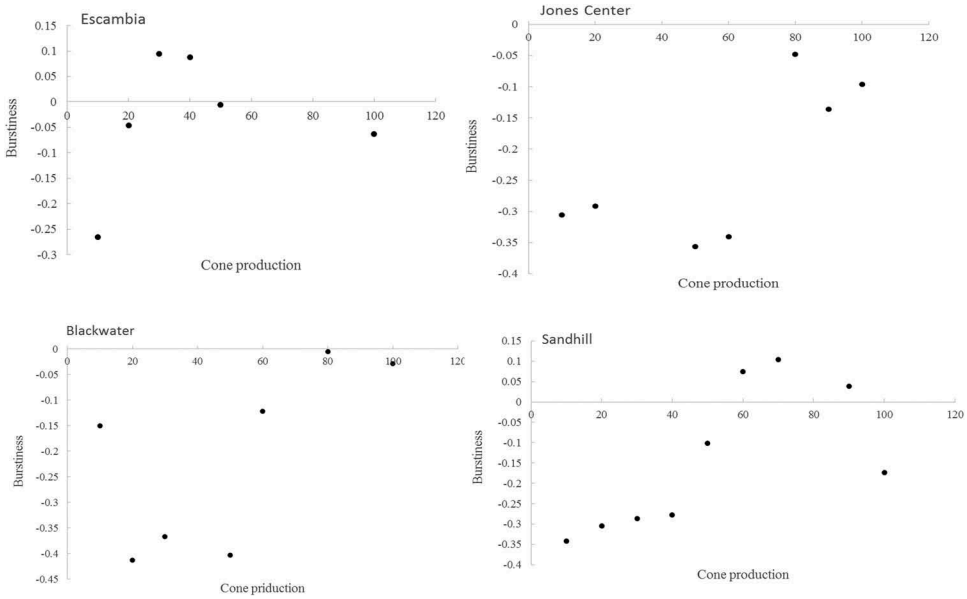

Figure 2. Dynamics of burstiness for cone production in longleaf pine forests at four sites.

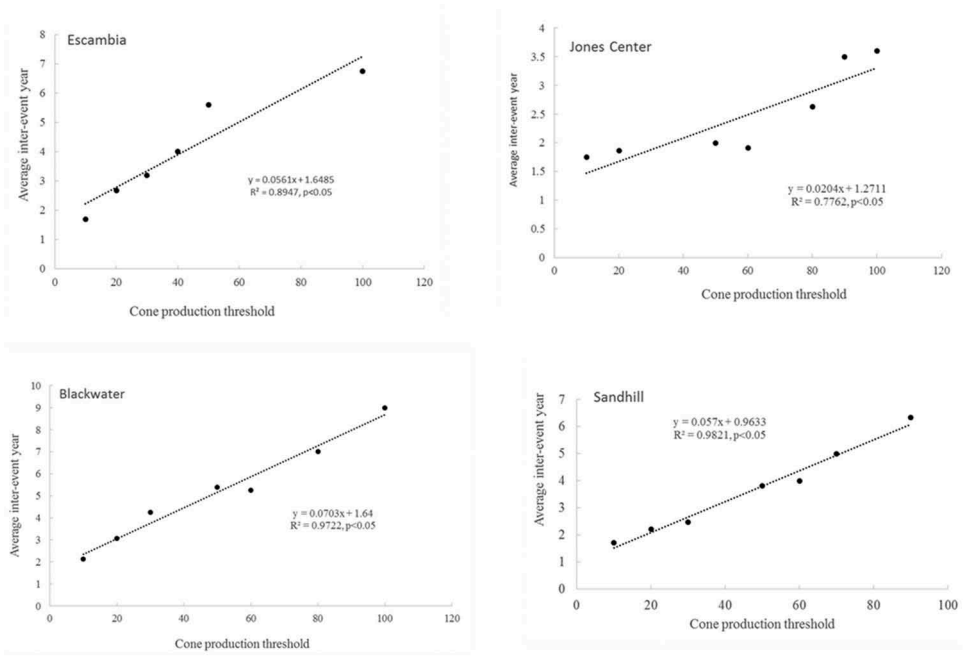

Figure 3. Correlation between cone production threshold and average inter-event time for longleaf pine at four sites.

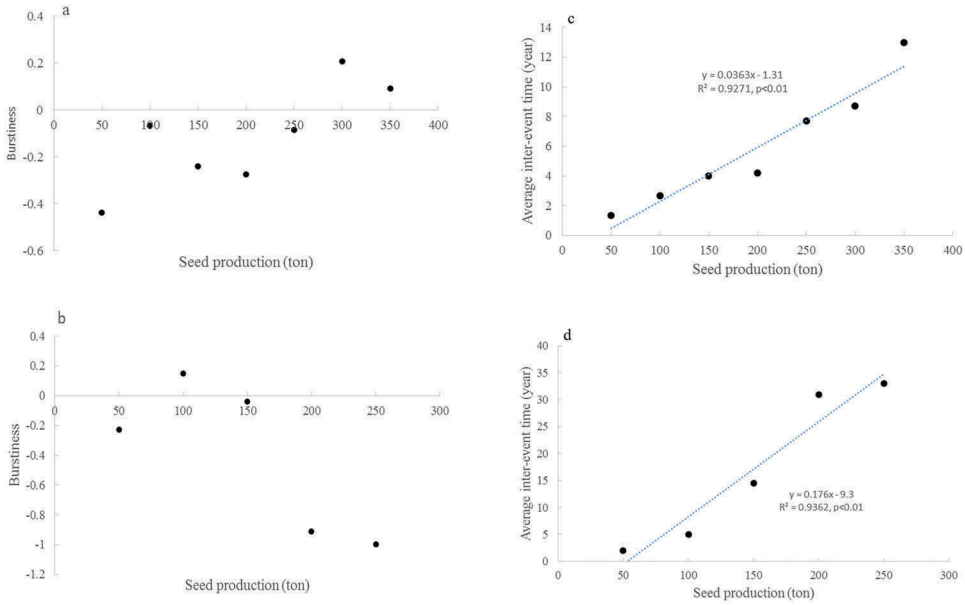

Figure 4. Dynamics of burstiness for seed production in Chinese Torreya at Zhaojiazhen of Zhuji City (a) and Jidongzhen of Shaoxing City (b); Correlation between seed production threshold and average inter-event time at Zhaojiazhen (c) and Jidongzhen (d).

which means that the dynamics of inter-event time was close to regular or periodic activity based on the concept of burstiness. Most values of burstiness were concentrated around −0.35 to 0.1 at these four sites. These values were relatively low, which means that the inter-event times in cone production were not very bursty. The origin of bursts in human behaviors (e.g., replying e-mail) was considered possibly due to priority in decision-making (Barabási, 2005). Cone production in longleaf pine forest may be also related to priority in resource allocation under the multiple driving forces. This is consistent with literature since cone production is a complex system influenced by climate and other factors.

We also analyzed pollen data at the Escambia site and found that the burstiness of pollen production was always negative along different thresholds (Figure 5). The scaling exponent (0.0005) between pollen production threshold and inter-event year was quite different from the scaling exponent (0.0561) between cone production and inter-event year. It appeared that the burstiness of pollen production had no direct correlation with the burstiness of cone production. Usually, the inter-event time was long for high cone production (e.g., ≥100 cones), but the inter-event year for higher cone production was relatively shorter at the Jones Center than at other sites.

Similar to burstiness in cone production for longleaf pine, the burstiness values of seed production for Chinese Torreya also ranged between low negative and low positive. The dynamics for burstiness of seed production were different between the two sites (Zhaojiazhen and Jidongzhen). Zhaojiazhen showed a shorter inter-event year and higher seed production for Chinese Torreya than did Jidongzhen.

Although having different scaling exponents, the scaling relationships between different thresholds of seed (cone) production and the average inter-event year were

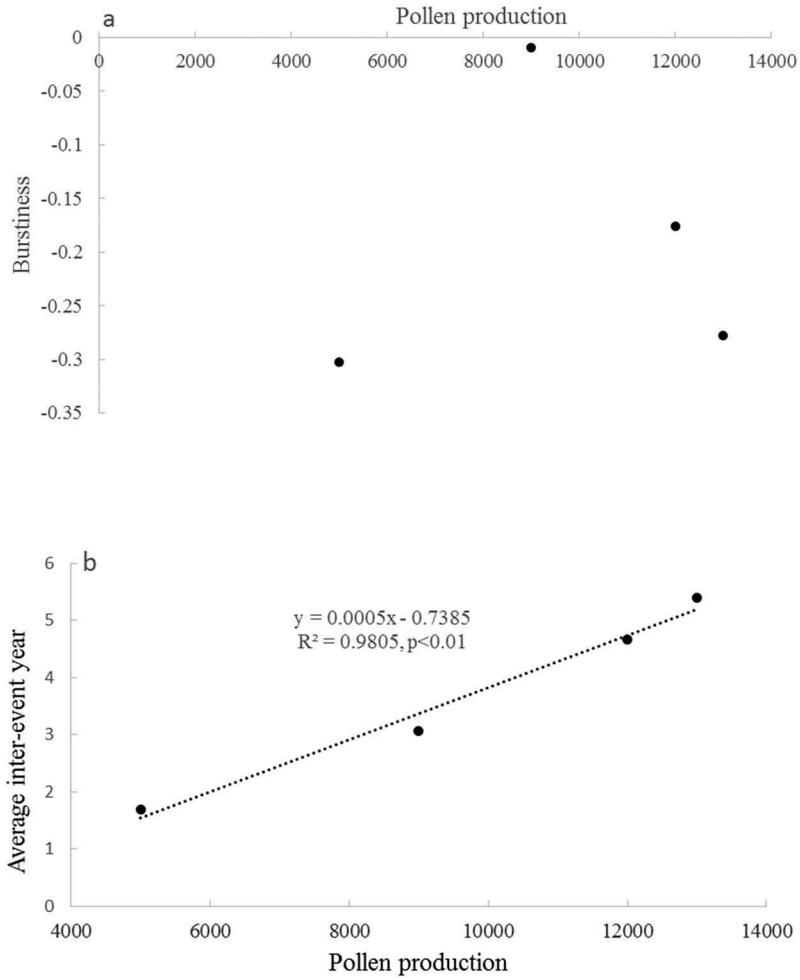

Figure 5. Dynamics of burstiness of pollen production (a) and the correlation between pollen production threshold and average inter-event time in pollen production for longleaf pine forest at the Escambia site (b).

found for these two tree species. Therefore, these trees might have a common intrinsic character in seed (cone) production, even though they are quite different species and also from different continents. The resource accumulation hypothesis suggested that trees need to accumulate resources for several years until a threshold is reached and then a big production occurs, which means a large amount of seeds will be produced with a certain biological periodicity (Kelly & Sork, 2002). This scaling relationship may provide a tool useful for estimating the time for the next episode of high seed (cone) production at each site. It can also help to identify locations having short inter-event times for high seed production, such as the Jones Center for longleaf pine and Zhaojiazhen for Chinese Torreya. However, the limitation of this approach is that long-term observational data, which most trees may not have, are needed to estimate the burstiness and scaling relationship in seed production.

Conclusion

Burstiness can be a useful index for characterizing the temporal inhomogeneity of seed production for trees with highly variable seed production. It can identify under what thresholds or in what time periods seed (cone) production has burst over a long time series. There exists scaling relationships between seed (cone) production and inter-event time for both longleaf pine and Chinese Torreya. The scaling relationships provide an estimate of average inter-event time for high seed production. Comparing the scaling relationships at different locations may help to find the sites with low inter-event time for high seed production. Studying the burstiness of tree seed production may discover new knowledge about trees and their seed production behaviors, which can be useful for sustainable forest management, such as estimating the effects of diseases and disturbances. These findings also indicate complex seed production systems may be governed by generic principles common to a number of species.

Disclosure statement

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References

Barabási, A.-L. (2005). The origin of bursts and heavy tails in human dynamics. *Nature*, *435*(7039), 207–211. https://doi.org/10.1038/nature03459

Brockway, D. G., Outcalt, K. W., & Boyer, W. D. (2006). Longleaf pine regeneration ecology and methods. In S. Jose, E. J. Jokela, & D. L. Miller (Eds.), *The longleaf pine ecosystem: Ecology, silviculture, and restoration* (pp. 95–133). Springer.

Campbell, D. R., & Halama, K. J. (1993). Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology*, *74*(4), 1043–1051. https://doi.org/10.2307/1940474

Chen, X., Brockway, G. D., & Guo, Q. (2016b). Entropy dynamics in cone production of longleaf pine forests in the southeastern United States. *Mathematical and Computational Forestry & Natural-Resource*, *8*(2), 11–15.

Chen, X., Brockway, G. D., & Guo, Q. (2018). Characterizing the dynamics of cone production for longleaf pine forests in the southeastern United States. *Forest Ecology & Management*, *429*, 1–6. https://doi.org/10.1016/j.foreco.2018.06.014

Chen, X., & Chen, H. (2019). Dynamics in production of four heritage foods at the mountainous region of Shaoxing City, China. *Emirates Journal of Food and Agriculture*, *31*(8), 645–653. https://doi.org/10.9755/ejfa.2019.v31.i8.1997

Chen, X., Guo, Q., & Brockway, D. G. (2016a). Analyzing the complexity of cone production in longleaf pine by multiscale entropy. *Journal of Sustainable Forestry*, *35*(2), 172–182. https://doi.org/10.1080/10549811.2015.1135294

Chen, X., Guo, Q., & Brockway, D. G. (2017). Power laws in cone production of longleaf pine across its native range in the United States. *Sustainable Agriculture Research*, *6*(4), 64–73. https://doi.org/10.5539/sar.v6n4p64

Chen, X., & Jin, H. (2019). Review of cultivation and development of Chinese torreya in China. *Forests, Trees, & Livelihoods*, *28*(1), 68–78. https://doi.org/10.1080/14728028.2018.1553690

Datlowe, D. W., Elcan, M. J., & Hudson, H. S. (1974). OSO-7 observations of solar X-rays in the energy range 10–100 keV. *Solar Physics*, *39*(1), 155–174. https://doi.org/10.1007/BF00154978

Dezsö, Z., Almaas, E., Lukács, A., Rácz, B., Szakadát, I., & Barabási, A.-L. (2006). Dynamics of information access on the web. *Physical Review E*, *73*(6), 066132. https://doi.org/10.1103/PhysRevE.73.066132

Eckmann, J. P., Moses, E., & Sergi, D. (2004). Entropy of dialogues creates coherent structures in e-mail traffic. *Proceedings of National Academy of Sciences USA*, *101*(40), 14333–14337. https://doi.org/10.1073/pnas.0405728101

Goh, K.-I., & Barabási, A.-L. (2008). Burstiness and memory in complex systems. *Europhysics Letters*, *81*(4), 48002. https://doi.org/10.1209/0295-5075/81/48002

Golding, I., Paulsson, J., Zawilski, S. M., & Cox, E. C. (2005). Real-time kinetics of gene activity in individual bacteria. *Cell*, *123*(6), 1025. https://doi.org/10.1016/j.cell.2005.09.031

Guo, Q., Brockway, D. G., & Chen, X. (2017). Temperature-related sex allocation shifts in a recovering keystone species, *Pinus palustris*. *Plant Ecology & Diversity*, *10*(4), 303–310. https://doi.org/10.1080/17550874.2017.1402968

Guo, Q., Zarnoch, S. J., Chen, X., & Brockway, D. G. (2016). Life cycle and masting of a recovering keystone indicator species under climate change. *Ecosystem Health & Sustainability*, *2*(6), e01226. https://doi.org/10.1002/ehs2.1226

Ito, H., & Nishinari, K. (2015). Universal bursty behavior in the air transportation system. *Physical Review E*, *92*(6), 062815. https://doi.org/10.1103/PhysRevE.92.062815

Janzen, D. H. (1969). Seed-eaters verses seed size, number, toxicity and dispersal. *Evolution*, *23*(1), 1–27. https://doi.org/10.1111/j.1558-5646.1969.tb03489.x

Janzen, D. H. (1976). Why bamboo wait so long to flower? *Annual Review of Ecology & Systematics*, *7*(1), 347–391. https://doi.org/10.1146/annurev.es.07.110176.002023

Kelly, D. (1994). The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution*, *9*(12), 465–470. https://doi.org/10.1016/0169-5347(94)90310-7

Kelly, D., & Sork, V. L. (2002). Mast seeding in perennial plants: Why, how, where? *Annual Review of Ecology & Systematics*, *33*(1), 427–447. https://doi.org/10.1146/annurev.ecolsys.33.020602.095433

Koenig, W. D., Mumme, R. L., Carmen, W. J., & Stanback, M. T. (1994). Acorn production by oaks in central coastal California: Variation within and among years. *Ecology*, *75*(1), 99–109. https://doi.org/10.2307/1939386

Li, Z.-J., & Dai, W.-S. 2007. *Chinese Torreya* in Chinese. Science Press.

Sork, V. L., Bramble, J., & Sexton, O. (1993). Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology*, *74*(2), 528–541. https://doi.org/10.2307/1939313

Thurner, S., Feurstein, M. C., & Teich, M. C. (1998). Multiresolution wavelet analysis of heartbeat intervals discriminates healthy patients from those with cardiac pathology. *Physical Review Letters*, *80*(7), 1544. https://doi.org/10.1103/PhysRevLett.80.1544

Vazquez, A., Rácz, B., Lukács, A., & Barabási, A.-L. (2007). Impact of non-Poissonian activity patterns on spreading processes. *Physical Review Letters*, *98*(15), 158702. https://doi.org/10.1103/PhysRevLett.98.158702