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Cover Caption: The woody bamboo *Bambusa bambos*, which flowers in collective synchrony every 32 years  
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## LETTER

# Extended flowering intervals of bamboos evolved by discrete multiplication

Carl Veller,<sup>1,2\*</sup>  
Martin A. Nowak<sup>1,2,3</sup> and  
Charles C. Davis<sup>2,\*</sup>

### Abstract

Numerous bamboo species collectively flower and seed at dramatically extended, regular intervals – some as long as 120 years. These collective seed releases, termed ‘masts’, are thought to be a strategy to overwhelm seed predators or to maximise pollination rates. But why are the intervals so long, and how did they evolve? We propose a simple mathematical model that supports their evolution as a two-step process: First, an initial phase in which a mostly annually flowering population synchronises onto a small multi-year interval. Second, a phase of successive small multiplications of the initial synchronisation interval, resulting in the extraordinary intervals seen today. A prediction of the hypothesis is that mast intervals observed today should factorise into small prime numbers. Using a historical data set of bamboo flowering observations, we find strong evidence in favour of this prediction. Our hypothesis provides the first theoretical explanation for the mechanism underlying this remarkable phenomenon.

### Keywords

Bamboos, biological clocks, masting, phenology.

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## INTRODUCTION

Understanding the basis of species’ phenology – the timing of life history events such as plant flowering and bird migration – is a key area of ecological and evolutionary research (Visser 2008). Easily one of the most captivating phenomena in this regard is the extended synchronous flowering and fruiting intervals exhibited by woody bamboos (Janzen 1976; Gould 1977). Although numerous woody bamboo species flower and fruit at more modest time intervals, there are many extraordinary examples of bamboos with greatly extended intervals (Fig. 1). For example, the Asian bamboos *Bambusa bambos*, *Phyllostachys nigra* f. *henonis* and *P. bambusoides* flower every 32, 60 and 120 years, respectively (Schimper 1903; Seifriz 1923, 1950; Kawamura 1927; Numata 1970; Chen 1973; Janzen 1976). Historical records of this phenomenon for the latter two species date back as far as 813 C.E. and 999 C.E. respectively (Kawamura 1927). In each of these cases, individuals of a species collectively flower and fruit in enormous quantities (referred to as ‘masting’) only to die back, leaving behind seeds which subsequently germinate. The cycle then repeats itself. In some documented cases, this synchrony is maintained even after plants are transplanted far from their native ranges (Morris 1886; Brandis 1899; Seifriz 1923; Chen 1973).

Though other plant species exhibit an ability to mast – most notably Dipterocarpaceae in Southeast Asia (Janzen 1974; Ashton *et al.* 1988) – none is known to exhibit either the regularity or the extraordinary interval length of the mast cycles observed in bamboos. Despite its broad interest to

biologists, however, the evolution of these prolonged regular flowering intervals has received surprisingly little theoretical investigation.

The leading explanation for masting in bamboos is attributed to Janzen (1974, 1976), who proposed that the enormous number of propagules (fruits or seeds) released during these episodes satiate local predator populations, ensuring that more seeds survive than with sporadic, and thus less abundant, propagule release (Kelly 1994; Kelly & Sork 2002). In the case of bamboos, these predators typically include rats, birds and pigs (Janzen 1976). The stabilising selection underlying the predator satiation hypothesis requires that a plant releasing its propagules out of synchrony with its cohort will likely have them all consumed by predators. Support for this comes from measurements of seed predation rates during and outside of masting episodes, including for bamboos (Kitzberger *et al.* 2007) and other masting species (Nilsson & Wästljung 1987; Crawley & Long 1995; Wolff 1996; Curran & Leighton 2000).

A second explanation for bamboo masting is that, in wind-pollinated plants like bamboos, synchronous pollen production may increase outcross pollination rates, providing a benefit to individuals who seed during a mast episode (Nilsson & Wästljung 1987; Norton & Kelly 1988; Smith *et al.* 1990). Evidence for this hypothesis comes from the higher fertilisation rates typically observed during mast episodes in wind-pollinated plants, including beech (Nilsson & Wästljung 1987), rimu (Norton & Kelly 1988), and oak (Koenig *et al.* 1994).

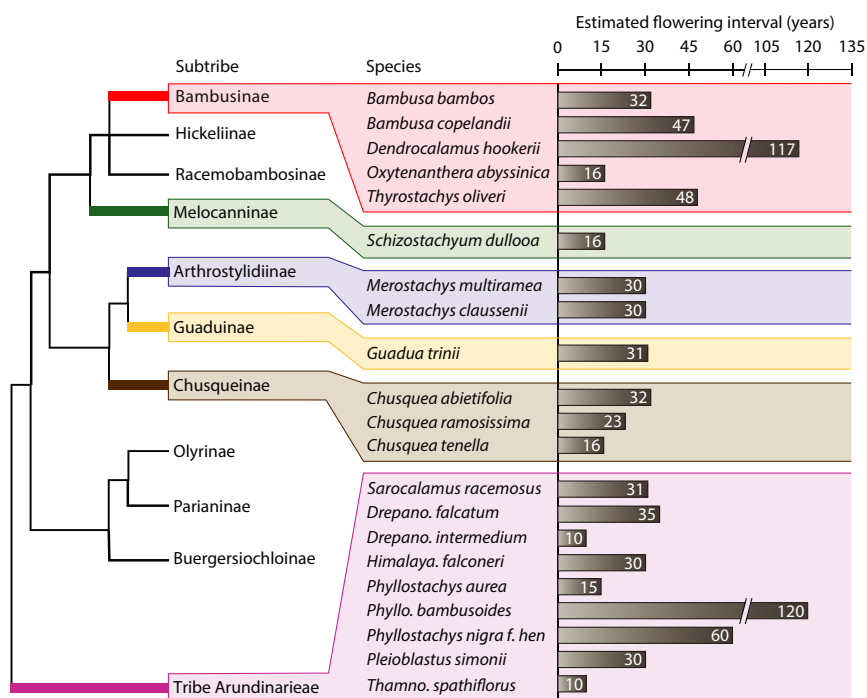
A third explanation, the so-called fire cycle hypothesis (Keeley & Bond 1999), argues that the large seed release

<sup>1</sup>Program for Evolutionary Dynamics, Harvard University, Cambridge, Massachusetts, 02138, USA

<sup>2</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, 02138, USA

<sup>3</sup>Department of Mathematics, Harvard University, Cambridge, Massachusetts, 02138, USA

\*Correspondence: E-mail: carlveller@fas.harvard.edu (or) E-mail: cdavis@oeb.harvard.edu



**Figure 1** Long-intervalled flowering in bamboos. A recent phylogeny of the bamboos as inferred by Kelchner (2013). Twenty-one species with long-intervalled flowering are displayed across their associated bamboo tribes and subtribes. These are species whose flowering intervals can be estimated from the data summarised by Janzen (1976) (see Appendix S3 for details of interval estimation). Species names have been updated to reflect current taxonomy.

during a mast can act as fuel for wildfires (sparked by lightning, for example). Under this scenario, bamboo seeds are hypothesised to be resilient to fire, while competing vegetation is not. However, most masting bamboo species live in humid, tropical forests, where wildfires are unlikely to have been a factor in their long-term evolution (Saha & Howe 2001). Moreover, it is difficult to see how the stabilising selection required for continued synchrony could be maintained without wildfires recurring frequently and predictably. The predator satiation and wind-pollination hypotheses, on the other hand, clearly involve perpetual stabilising selection.

While these theories of stabilising selection provide explanations for the existence of synchronous seeding in bamboos, a more intriguing puzzle remains: what explains the remarkable regularity and length of bamboo mast cycles? Here, we propose and test a novel mathematical model of the evolution of bamboo masting to solve this puzzle. The puzzle is twofold. First, how was synchrony achieved on the shorter, regular multi-year intervals that have been hypothesised to be ancestral in bamboos (Janzen 1976)? Second, given the strong stabilising selection for maintaining a regular interval, how did the shorter ancestral intervals lengthen to the extraordinary intervals seen today?

In the mathematical models we develop to answer these questions, we shall primarily make use of the language of the predator satiation hypothesis, simply because it is the best known and most widely accepted explanation for masting in bamboos. The models do not depend on the veracity of the predator satiation hypothesis, however, only on the existence of stabilising selection. In general, they can be written in the language of any of the theories of stabilising selection

proposed for bamboo masting, including the commonly invoked wind-pollination hypothesis.

## MODEL OF INITIAL SYNCHRONISATION

We first hypothesised that initial synchronisation on a multi-year interval could occur naturally in a population of annual flowerers when two conditions are met. First, plants that wait longer to flower may accumulate greater energy resources to invest in producing more seeds, and/or seeds that are better protected (Fenner 1985). (The latter scenario, involving better-protected seeds, seems less applicable to bamboos, whose ancestral fruit type is a caryopsis, i.e. fruits with seeds that are generally less well protected than those of many other flowering plants.) In bamboos, this investment might, for example, take the form of increased shoot production between masts. Second, total potential seed predation varies from year to year, but is typically high, amounting to a significant proportion of maximum possible seed release. Evidence for this assertion comes from observations of enormous predation rates in minor mast years among well-studied woody tree species (Nilsson & Wästljung 1987; Crawley & Long 1995; Wolff 1996; Curran & Leighton 2000).

These conditions can be incorporated into a simple mathematical model (Fig. 2; full mathematical details in Appendix S1). Here, we assume a fixed environmental carrying capacity, and begin with a population comprising mostly plants that seed annually, but with some variation in seeding time, so that a small number of plants seed every 2 years. These 2-year plants may be distributed across odd and even years in this 2-



year cycle, forming two reproductively distinct ‘cohorts’. Under a broad class of parameterisations, a common outcome of our model is synchronisation onto a single cohort of 2-year plants, following a year where all annual plants and one cohort of 2-year plants are eliminated because their entire seed set is lost to predation (see Fig. 2 for additional details of the population dynamics involved).

Importantly, our model is not restricted to synchronisation onto only a 2-year cycle: longer intervals of synchronisation are possible in a similar model if we extend the variation in the initial population to include plants with longer flowering intervals, including three, four and five years (Fig. 3). Also, by altering the parameters of the model, we can hasten or lengthen the transition to a multi-year mast cycle, so that the transition times in Figs. 2 and 3 should not be seen as characteristic of the model (see Appendix S1).

### MODEL OF INTERVAL GROWTH BY MULTIPLICATION

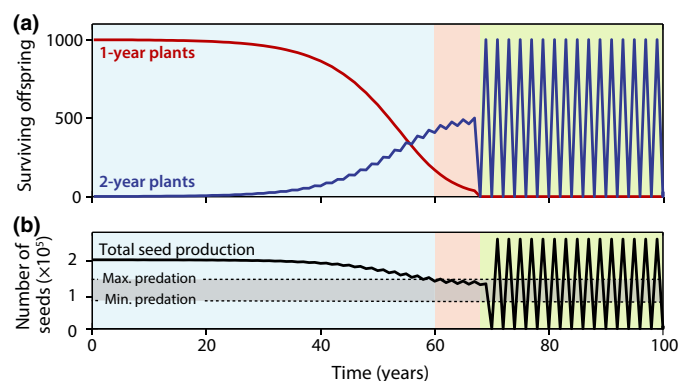
Once synchronisation has been established in a population, say, on a 3-year mast interval, stabilising selection should maintain synchrony. This is because a plant flowering out of sync – for example, after 2 or 4 years – would release its seeds alone, and thus have its entire seed set consumed by predators. Given such strong selection for synchrony, how then could flowering intervals have increased to the extraordinary lengths observed today? Janzen (1976) noted that a plant flowering at an interval twice that of its population – at 6 years, in the case of a 3-year population mast cycle – would always flower during a masting year (i.e. every second mast), and thus be buffered against predation. Indeed, this holds for a mutant flowering at any multiple of the initial population mast interval, not just double. And since plants waiting longer to flower release more propagules, such mutants would likely be favoured during times of low population growth, when delaying seeding would not represent a significant ‘missed opportunity’.

For example, suppose a mutant with a flowering interval twice that of its population releases  $s\%$  more seeds than the average single-interval plant (or, equivalently, seeds that are better protected, and thus suffer  $s\%$  less predation). Suppose too that average population growth is  $g\%$  per period. Then a simple population growth model predicts that selection will favour the mutant if  $s > g$ . Over two population masts, an average population member will yield  $(1 + g)^2$  descendants, while the mutant will yield  $(1 + g)(1 + s)$  descendants; the latter is larger than the former when  $s > g$ . This is likely to hold especially when population growth,  $g$ , is low (and owing to the nature of exponential growth,  $g$  cannot be large for too extended a period of time). Analogous conditions for mutants of higher multiple intervals can also be derived. In general, if the population growth rate is  $g\%$ , a mutant that flowers only every  $n$  mast periods and releases  $s_n\%$  more seeds than the average population member will face positive selection if  $1 + s_n > (1 + g)^{n-1}$ . For small integers  $n$ , this is likely to hold for reasonable long-term values of  $g$ . So when population growth is low, multiple-interval mutants can emerge, be selected for, and fix. Under this scenario, the population’s

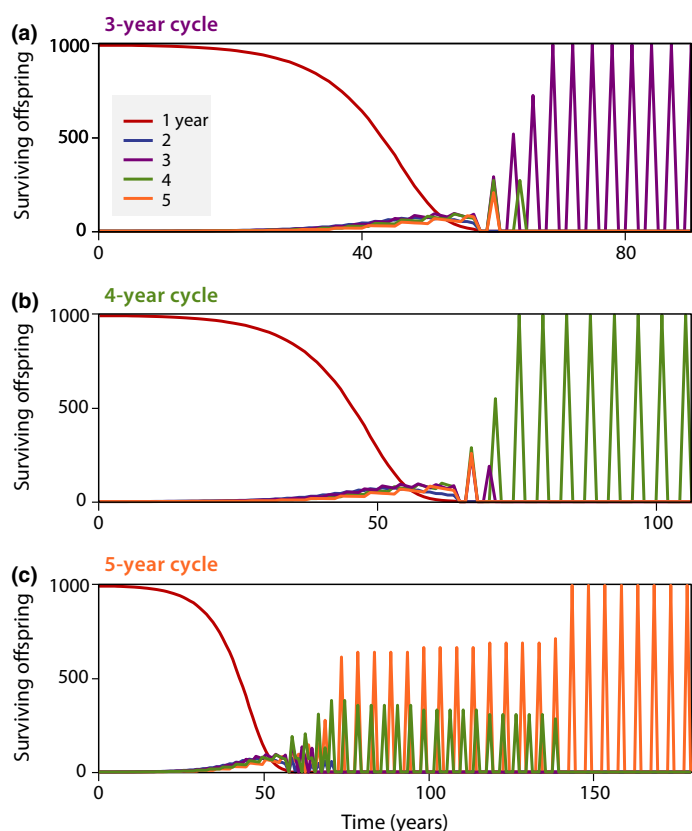
flowering period increases to a multiple of its initial synchronisation interval.

The converse, however, is not true: if a population’s growth rate increases, mutants with intervals a fraction – say half – of the cohort’s would not survive, because they would seed out of sync with the population every second period of their reduced interval. So, earlier initial flowering intervals are not recoverable, and thus the population’s flowering interval can only increase in our multiplicative model. The evolution of extended flowering intervals in bamboos may therefore represent an instance of Dollo’s law, or irreversibility in evolution (Dollo 1893).

The rival hypothesis for the evolution of very long mast intervals is one of gradual growth. Because mast episodes are not instantaneous, instead lasting from a few weeks to even a few years in the case of species with very long mast intervals, such as *Phyllostachys bambusoides* (Janzen 1976), seed release is in fact distributed across a mast episode. If plants that release their seeds later in the episode are selectively favoured, then selection over time would gradually shift the distribution in the direction of longer intervals. However, both theory and empirical evidence suggest that plants releasing their seeds later in mast episodes would in fact be selected *against*. Since mast episodes tend to result in a surge in local seed predator populations, either through migration or rapid reproductive growth, predation pressure is expected to increase as a mast episode progresses. Seeds released late in a mast are thus expected to suffer the highest predation rates, and yield fewer successful offspring (Janzen 1976). This is borne out in studies that observe predation rates across entire mast episodes, both



**Figure 2** A model of initial synchronisation in bamboos. Blue phase: Initially, the population comprises mostly annual-flowering bamboos, with a small number flowering every 2 years (symmetric across odd and even years). Owing to their higher individual seed release, the 2-year plants increase in numbers over time (a). Total annual seed release declines, as the population’s seeding becomes increasingly diluted over the odd and even years of the 2-year cohorts (b). Red phase: When total annual seed release declines below maximum potential predation (b), the population is at risk of having an annual seed release completely consumed by predators. When this eventually occurs, all of the annual plants, together with the 2-year cohort seeding that year, are eliminated (a). Green phase: If predation is not unusually high the following year, the seed release of the remaining 2-year cohort will fill the environmental carrying capacity, establishing synchrony onto that cohort’s 2-year cycle.



**Figure 3** Initial evolution of mast intervals longer than 2 years. Our model of initial synchronisation can also explain the initial evolution of mast intervals longer than 2 years, if sufficient variation exists in the original (mostly annual-flowering) population. Because of the stochastic nature of the model, the same original setup can result in the evolution of a 3 year (a), 4 year (b) or 5 year (c) mast cycle.

for bamboos (Gonzalez & Donoso 1999; Kitzberger *et al.* 2007) and for Dipterocarpaceae (Curran & Leighton 2000; Curran & Webb 2000).

On the other hand, seeds released early in a mast episode do not enjoy the safety in numbers that seeds released during the mast's peak do. Despite predator levels initially being low, therefore, these early seeds are very vulnerable to predation by the predators that are present. Thus, while the above argument against gradual interval growth suggests that gradual interval reduction is a possibility, we do not expect such reductions to significantly affect mast interval lengths.

It has been claimed that the very long mast intervals observed in, for example, *Phyllostachys bambusoides* (120 years) and *P. nigra* f. *henonis* (60 years) constitute evidence against the predator satiation hypothesis (Keeley & Bond 1999). It has been assumed that integral to the hypothesis is that long mast intervals have evolved to starve seed predators between masts, ensuring that predator numbers are low when a mast eventually occurs (Janzen 1976; Kelly 1994; Kelly & Sork 2002). But since the longest known mast intervals greatly exceed the lifespans of typical seed predators, the predator satiation hypothesis cannot alone explain why selection favoured increases of mast intervals to the extremes

observed today (Keeley & Bond 1999). This argument similarly pits these observations against other theories of stabilising selection, such as the wind-pollination hypothesis. In our theory of interval growth by successive multiplication, we have reconciled the predator satiation hypothesis (and, indeed, any theory of stabilising selection) with the existence of extreme mast interval lengths. Though the key selective factor in longer intervals is greater seed release, rather than predation (or any other stabilising factor), that these longer intervals must be discrete multiples of their preceding intervals is a direct result of the heavy predation faced by plants releasing their seeds in isolation (or, again, any perpetual stabilising force that maintains synchrony).

### STATISTICAL TESTING

The logic underlying this mechanism of interval growth yields a simple, testable numerical prediction. If the extraordinary flowering intervals observed today are the result of successive multiplications of the initial synchronisation interval, then they should be decomposable back into those multiples (and the initial interval). Though the theory is consistent with multiples of any size if population growth is sufficiently low, and though the mechanics of the genetic clock in bamboos are poorly understood (Nadgauda *et al.* 1990), small multiples seem more likely than larger ones. The physiological and underlying genetic adjustments necessary for much larger single-interval multiplications would likely render such multiplications implausible. Thus, we hypothesise that the extended mast intervals of bamboos should factorise into small positive integers, so that their unique prime factorisation should include only small prime numbers.

Do the data support this hypothesis? An initial survey of the most well-studied examples is promising (Fig. 1): *Phyllostachys bambusoides* (120 years = 5 year initial synchronisation interval  $\times 3 \times 2 \times 2 \times 2$ ), *P. nigra* f. *henonis* (60 years = 5 years  $\times 3 \times 2 \times 2$ ), and *Bambusa bambos* (32 years = 2 years  $\times 2 \times 2 \times 2 \times 2$ ) (Schimper 1903; Seifriz 1923, 1950; Kawamura 1927; Numata 1970; Chen 1973; Janzen 1976). These examples support our hypothesis on several fronts. First, all of these intervals are factorisable into small primes (5 or smaller). Second, the smallest primes appear most often in each factorisation, consistent with smaller prime multiples being more likely. Third, the 120 year mast interval of *P. bambusoides* is a small multiple of the 60 year interval of the closely related *P. nigra* f. *henonis*, suggesting a common ancestral interval from which the two have evolved.

Other bamboo species with extended intervals are less well studied. For these species, a number of factors are likely to increase measurement error in estimates of mast intervals (Janzen 1976). These include geographic variation in observations of masting, observations gathered at different stages of consecutive masting episodes (many of which can last more than 1 year), and misidentification of species, as well as natural variation around mean flowering intervals within species (Franklin 2004). A more detailed discussion of the factors that contribute to mast interval measurement error is included in Appendix S2.

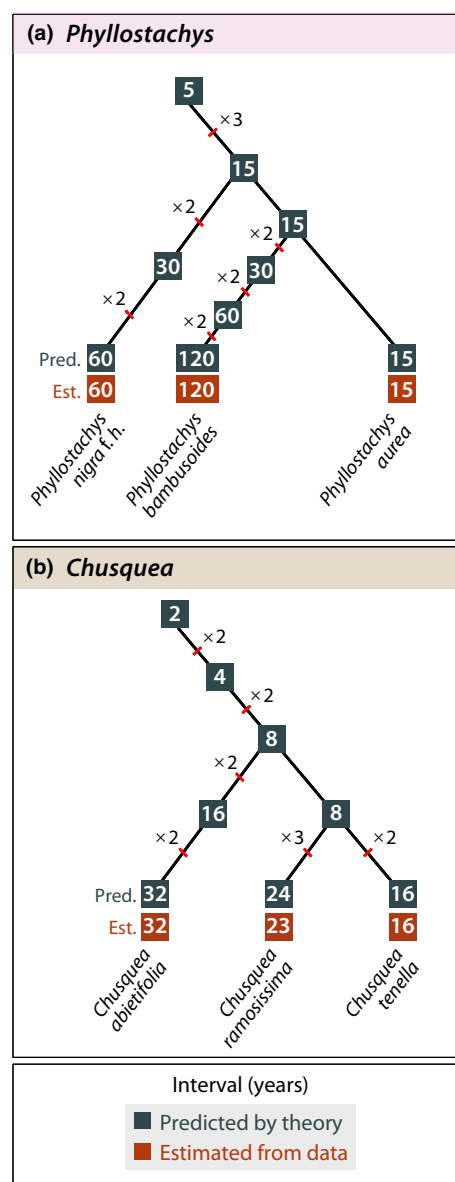
Nonetheless, a broader inspection of the estimated mast intervals of these less well-studied species, together with their phylogenetic placement, corroborates our hypothesis. In the two monophyletic genera in our data that exhibit variation in mast intervals across more than two species, *Phyllostachys* and *Chusquea*, these mast intervals show evidence of having arisen through a multiplicative process (Fig. 4). The three *Phyllostachys* species in our data share a common base interval of 15 years (15 years, 60, 120), which under our hypothesis would itself have arisen from a shorter (3 or 5 years) initial synchronisation interval. Allowing for measurement error, the three *Chusquea* species appear to share a base interval of 8 years (16 years, 23, 32). Similar patterns of multiples in bamboo flowering intervals have previously been noted as anomalous (Guerreiro 2014) – this anomaly is resolved as a natural consequence of our multiplication model.

To test our hypothesis more formally, we developed a simple, robust nonparametric test to determine if estimated mast intervals (Fig. 1) are more tightly clustered around numbers factorisable into small primes ('NFSP', here defined as primes 5 or smaller) than would be expected by chance under an appropriate null hypothesis. Here, our null hypothesis is that extended mast intervals evolved gradually (instead of via the discrete multiplications we have hypothesised), resulting in a smooth, continuous distribution of interval lengths (see Appendix S3 for details of the estimation of the null distribution). Compared to samples generated from this null distribution, the measured flowering intervals are significantly closer to NFSP ( $P = 0.0041$ ) and contain significantly more NFSP ( $P = 0.0024$ ). These results strongly support our hypothesis. Moreover, they are robust to changes in the construction of the null distribution, and alternative definitions of NFSP (see Appendix S3).

## DISCUSSION

To our knowledge, our study is the first to develop a mathematical theory of the mechanism underlying extended mast intervals in bamboos. In our model, an initial phase of synchronisation onto a small interval is followed by successive multiplication of the interval by small numbers. Three key assumptions underlie our multiplication model: (1) strong stabilising selection that maintains interval synchrony, (2) that later seed release allows for greater seed release (and/or for better-protected seeds) and (3) approximately regular, endogenously timed mast intervals. These assumptions may explain why other masting plant species, such as members of the Dipterocarpaceae clade, do not exhibit such greatly extended intervals as the bamboos do. In particular, while assumptions (1) and (2) above are likely to apply to many masting plants, assumption (3), which is likely under genetic regulation, appears to be unique to bamboos. This assumption, which is crucial to the survival of multiple-interval mutants in our model, may thus be the key distinction that has allowed bamboos to achieve such dramatically extended flowering intervals.

The only other organisms that are well known to exhibit regular long-interval synchrony are the periodical cicadas (genus *Magicicada*), whose synchronised emergence from an



**Figure 4** Mast intervals within bamboo subclades appear to have arisen from a multiplication process. Two hypothesised patterns of small multiplications of intervals along phylogenies (Fisher *et al.* 2009; Triplett & Clark 2010) of *Phyllostachys* (a) and *Chusquea* (b), the two genera in our data set for which flowering intervals can be estimated for more than two species. The mast intervals of these species are consistent with the multiplication model we propose, allowing for small measurement error in the case of *C. ramosissima* (estimated interval 23 years vs. predicted interval 24 years). Hypothesised intervals, ancestral and extant, are displayed in boxes; measured intervals from our data set are displayed on the bottom lines.

underground larval state on 13- and 17-year intervals has similarly been attributed to predator satiation (Lloyd & Dybas 1966a,b; Bulmer 1977). Evolutionary explanations have been proposed for their large-prime lifecycles (May 1979; Yoshimura 1997; Goles *et al.* 2001), which clearly cannot be factorised into small primes, and thus stand in contrast to our hypothesis for the evolution of long-intervalled masting in bamboos. This suggests distinct evolutionary and genetic mechanisms underlying the periodical lifecycle of cicadas in



comparison to long-intervalled masting in bamboos. For example, a leading explanation for the large-prime lifecycles of the periodical cicadas is that they minimise the possible frequency of subharmonic resonances with the multi-year lifecycle of a predator or parasite (Williams & Simon 1995). This evolutionary mechanism appears not to apply to masting bamboos, since the major predators of their seeds are typically either fast-breeding (e.g. rats) or migratory (e.g. fowl and pigs).

In conclusion, our multiplicative model provides the first theoretical explanation of long-intervalled masting in bamboos, and offers a framework upon which comparative analyses can be devised to explore the genetic and developmental basis of this striking biological phenomenon.

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#### AUTHOR CONTRIBUTIONS

C.V. conceived of project. C.V. and C.C.D. designed research. C.V., M.A.N. and C.C.D. carried out research, and wrote the manuscript.

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# Extended flowering intervals of bamboos evolved by discrete multiplication

Carl Veller<sup>\*†§</sup>     Martin A. Nowak<sup>\*†‡</sup>     Charles C. Davis<sup>†§</sup>

## APPENDIX

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<sup>\*</sup>Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138

<sup>†</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138

<sup>‡</sup>Department of Mathematics, Harvard University, Cambridge, MA 02138

<sup>§</sup>Correspondence to: carlveller@fas.harvard.edu, cdavis@oeb.harvard.edu

# S1 Mathematical model of synchronization

In this section, we describe our synchronization model, the key results of which are displayed in Figs. 2 and 3 in the main text. First, we describe the general specification of the model. Second, we describe the particular parameter specifications used for the model, present the results of these specifications, and discuss the results in detail. We also demonstrate that the results are robust to significant changes in the parameter specifications.

## S1.1 General synchronization model

We assume a constant carrying capacity of  $K$  individuals (assigned to ‘stands’) throughout our synchronization models and simulations. Let  $X_{\tau,y}$  be the number of plants of flowering interval  $\tau$  (in units of integer years) present in year  $y$ , where  $\tau \in \{1, \dots, T\}$  and  $y = 1, 2, \dots$ . Assume that each annual plant releases  $S$  seeds in a flowering episode, and that plants of interval  $\tau$  each release  $f_{\tau}S$  seeds per episode. We invoke a standard assumption (Fenner, 1985) that plants of greater interval length release more seeds when they do eventually seed, i.e.,  $1 = f_1 < f_2 < \dots$ .

For each flowering interval  $\tau$ , there are  $\tau$  possible ‘cohorts’. These seed separately in years  $1, 2, \dots, \tau$ . Formally, we define individual cohorts thus: Let  $N_{\tau,y}$  be the number of bamboos of interval  $\tau$  starting life in year  $y$ . This is the number of seeds released by interval  $\tau$  plants in year  $y$  that germinate and survive to adulthood. We assume no mortality of adult plants until they seed (after which, being semelparous, they die), so for each  $\tau$ ,  $X_{\tau,y} = N_{\tau,y} + N_{\tau,y-1} + \dots + N_{\tau,y-\tau+1}$  (since the  $\tau, y - \tau$  cohort has just died giving rise to the  $\tau, y$  cohort).

Seed mortality occurs first from predation, and then, when applicable, from the fact that more seeds survive predation than can fill the remaining carrying capacity. Total potential predation in year  $y$  is  $\alpha_y SK$ , where  $\alpha_y \stackrel{\text{iid}}{\sim} U[\underline{\alpha}, \bar{\alpha}]$ . This corresponds to a proportion between  $\underline{\alpha}$  and  $\bar{\alpha}$  of the total seed release of a population of all annual plants. We shall assume this proportion to be significant, which is consistent with the enormous predation rates observed in minor mast years among bamboos (Kitzberger et al., 2007) and well-studied woody tree species (Nilsson and Wastljung, 1987; Curran and Leighton, 2000). If fewer seeds are released in a year than total potential predation in that year, all seeds are eaten, and the cohorts seeding that year are eliminated entirely from the population.

Finally, we assume predation of seeds of interval  $1, 2, \dots, T$  in year  $y$  to be proportional to the number of each released that year. Seeds of interval  $1, 2, \dots, T$  surviving predation are assigned to empty stands (i.e., the remaining carrying capacity) also in proportion to the number released (and thus also in proportion to the number of each surviving predation, from the previous sentence).

This is sufficient information to characterize the population dynamics, which we do now:

In year  $y$ , for each  $\tau$ , all plants of the cohort  $\tau, y - \tau$  release  $f_\tau S$  seeds each, and die. Total potential predation is  $\alpha_y SK$ . Thus:

- Total population seed release:  $S_y = \sum_\tau SN_{\tau, y-\tau} f_\tau$
- Proportion of seeds that are of interval  $\tau$ :  $p_{\tau, y} = SN_{\tau, y-\tau} f_\tau / S_y$
- Total number of seeds surviving predation:  $S_y^P = \max(S_y - \alpha_y SK, 0)$
- Carrying capacity remaining ('vacant stands'):  $V_y = K - \sum_\tau [X_{\tau, y-1} - N_{\tau, y-\tau}] \in [0, K]$ .

So,  $N_{\tau, y} = p_{\tau, y} \min(S_y^P, V_y)$ , and  $X_{\tau, y} = N_{\tau, y} + \dots + N_{\tau, y-\tau+1} = X_{\tau, y-1} + N_{\tau, y} - N_{\tau, y-\tau}$ .

## S1.2 Parameter specification for two-year synchronization model

For the baseline two-year synchronization model presented in the main text (Fig. 2), we assume a maximum flowering interval of  $T = 2$  years, a carrying capacity of  $K = 1000$  plants(/stands), and begin initially with a mostly annual population in years 1 and 2:  $X_{1,1} = 998$ ,  $X_{2,1} = 2$ ,  $X_{1,2} = 998$ ,  $X_{2,2} = 2$ . We assume an equal number of two-year plants in each of the two two-year cohorts ('odd' and 'even'), so that  $N_{2,1} = N_{2,2} = 1$ . Having initial symmetry between the two cohorts does not significantly change the probability that synchronization onto a two year interval will result. Initial asymmetry tends to result in synchronization onto the initially-larger cohort's cycle, with probability slightly lower than that of synchrony onto any two year cycle in the symmetric case (see robustness checks below).

$S$ , the number of seeds released in an episode by an annual plant, is a dummy variable, with no effect on the model once predation is defined as some multiple of it. We set it arbitrarily to 200. Plants flowering every two years release 30% more seeds than annual plants:  $f_2 = 1.3$ .

Total potential predation is distributed uniformly between 40% and 70% of the total seed release of an entirely annual population:  $\underline{\alpha} = 0.4$ ,  $\bar{\alpha} = 0.7$ . Having such a wide range of potential predation values is not necessary for synchronization to result in the model, but does make the mechanism by which synchrony results significantly clearer in our figures.

## S1.3 Results of two-year synchronization model

Under the specifications detailed above, two outcomes are possible from our model. The first, occurring in  $\sim 77\%$  of simulations, is synchronization of the population onto a two

year flowering interval (Fig. 2a in the main text, Fig. S1a here). The second, occurring in the remaining  $\sim 23\%$  of simulations, is extinction of the population (Fig. S1b).

It is easy to understand how each occurs in this model. First, we note that a population comprised only of two-year plants, with approximately equal numbers across the odd and even cohorts, cannot survive perpetually: in each year, only about half the population seeds, which amounts to a seed release of  $\sim 500 \times 1.3 \times S = 650S$ . The maximum yearly potential predation, on the other hand, is higher than this value, being  $0.7 \times 1000 \times S = 700S$ . Thus, in a year where potential predation is particularly high, the cohort seeding that year will experience total predation of its seeds, and be eliminated.

Initially, though, with a mostly annual population, most of the population seeds each year. Total seed release is then  $\sim 1000S > 700S$ , and so total predation is never a concern. Under these conditions, the two-year plants are protected from total predation, and their higher individual seed release ensures that they grow as a proportion of the population. As they do, though, the population gradually approaches the state described above where two year plants are a large proportion, and seeding becomes spread across the two cohorts. Thus, total annual seed release declines below the levels observed under

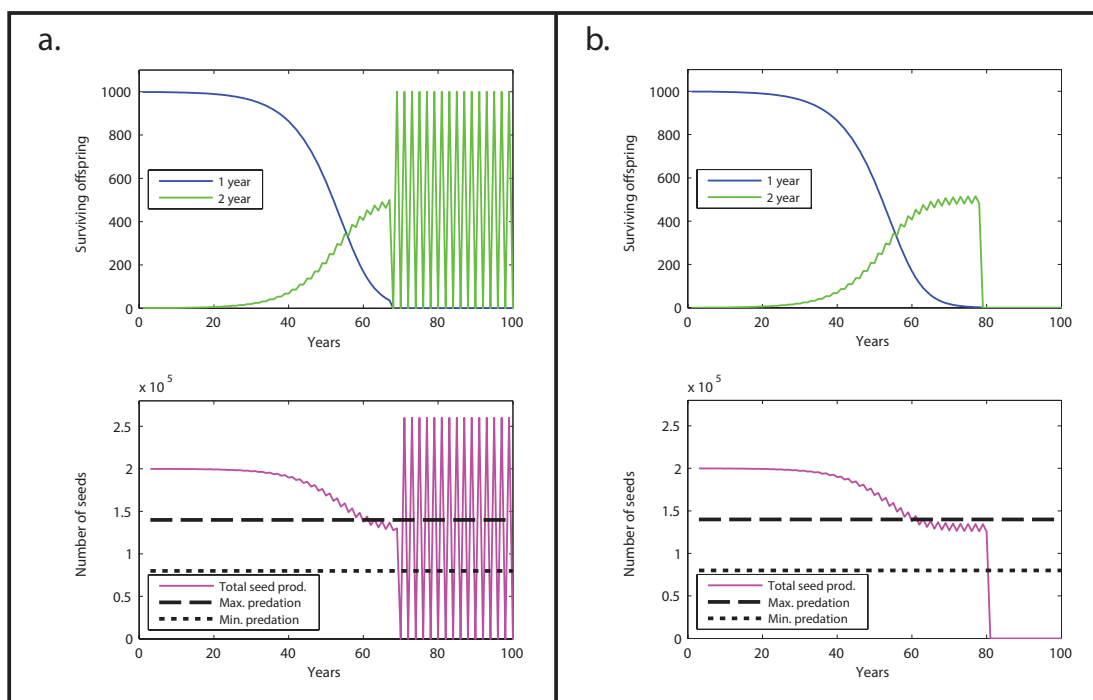


Figure S1: The two possible results of the synchronization model's population dynamics. **a.** Synchronization onto a two year interval (as presented in the main text). **b.** Extinction of the entire population.



the initial conditions.

Eventually, total annual seed release declines below  $700S$ , and total predation becomes a possibility. When it occurs, all of the annual plants, and the two-year cohort seeding that year (say, the ‘even’ cohort), are eliminated. This is where the two possible outcomes of the model are clearly observed. If total potential predation the next year is again very high, the other two-year cohort (the ‘odd’ cohort), releasing its seeds then without the extra buffer of the annual plants’ release (the annuals having been eliminated, though their numbers were small anyway), will also be eliminated, and the whole population will become extinct. On the other hand, if total potential predation the next year is not very high, the remaining two year cohort will release more seeds than can be eaten by predators, and the surviving seeds will exceed the carrying capacity of the environment (since total seed release is orders of magnitude higher than the carrying capacity, it is very unlikely that there will be fewer surviving seeds than the carrying capacity). 1000 two-year plants flowering in synch will never suffer total predation, since  $1.3 \times 1000 \times S > 700S$ , and so synchronization onto a two year interval will have been achieved, and will be sustained.

#### S1.4 Robustness of the two-year synchronization model

If we keep the requirement that the two two-year cohorts initially be of the same size, then the result that synchronization can occur is robust to changes in parameter specifications that maintain the following ‘rule of thumb’ properties of the model (precise conditions are not possible because of the stochasticity of the process):

- Total potential predation cannot exceed the amount of seeds released by a full population ( $K$ ) of only annual plants (or else extinction of the entire population will always occur early on).
- Total potential predation can sometimes be below, and sometimes exceed, the amount of seeds released by about a half population ( $K/2$ ) of two-year plants. That it can exceed this amount rules out the possibility that two separate cohorts of two-year plants can coexist perpetually. That it can be below allows for the possibility that, when the first instance of total predation occurs and eliminates the annual plants and one cohort of two-year plants, the other two-year cohort can release enough seeds the following year to avoid total predation.

It is important to note that, since the dynamics are stochastic, and since the number of annual plants left in the population at the time of first total predation changes from simulation to simulation, these requirements are not exact. The first requirement translates to  $\bar{\alpha} < 1$ . The second translates to  $\underline{\alpha}SK < f_2SK/2 < \bar{\alpha}SK$ , which simplifies to  $\underline{\alpha} < f_2/2 < \bar{\alpha}$ . So, the evolution of synchrony onto a two-year cycle is possible in our

model when  $\alpha < f_2/2 < \bar{\alpha} < 1$ . It is clear that these requirements will hold for a large number of parameter specifications.

Bearing these rough requirements in mind, we can see that, if two-year plants do not release many more seeds than one-year plants ( $f_2$  values lower than the value of 1.3 assumed above in our simulations), then the evolution of a two year cycle, still possible under the appropriate parameterizations, occurs after a longer period of time. This is because, with a lower selective advantage, it takes longer for two-year plants to occupy a large enough proportion of the population that total population seed production is below the maximum predation level. An example of this longer time until establishment of a two year cycle is given in Fig. S2a.

Allowing for asymmetry in numbers between the initial two two-year cohorts does not significantly alter the probability that synchronization onto a two year cycle results in the model. For example, beginning with five two-year plants in year 1 ('odd' cycle) and one two-year plant in year 2 ('even' cycle), and otherwise keeping the same parameter specification from Section S1.2, population synchronization onto the odd two-year cycle occurs in  $\sim 70\%$  of simulations, while synchronization onto the even two-year cycle essentially never occurs. Population extinction is the result in the remaining  $\sim 30\%$  of simulations, slightly higher than in the symmetric case.

Finally, we might expect the total potential predation in a given year to depend on the number of seeds released. For example, the predator population surges that typically accompany mast events might be more rapid when seed release is greater, leading to higher total predation pressure. On the other hand, since bamboo seed predators do feed solely on bamboo seeds, we should also expect a non-density-dependent component to total potential predation. To model this, let  $\alpha_b$  be a stochastic baseline (i.e., non-density-dependent) predation pressure, drawn independently each year from the uniform distribution on  $[0.1, 0.3]$ , and contributing  $\alpha_b KS$  potential predation each year. Let  $\alpha_d$  be a stochastic density-dependent predation pressure, drawn independently each year from the uniform distribution on  $[0.4, 0.6]$ , and contributing  $\alpha_d S_y$  predation pressure in a year where the total population seed release is  $S_y$ . Then the total predation pressure in year  $y$  is  $\alpha_b KS + \alpha_d S_y$ . Synchronization onto a two year cycle is possible under this model (Fig. S2b), with the logic the same as before.

### S1.5 Higher-interval synchronizations

Is synchronization onto an interval that is greater than two years possible? Maintaining a carrying capacity  $K = 1000$ , we allow a maximum interval in the population of  $T = 5$ , set  $(f_2, f_3, f_4, f_5) = (1.3, 1.5, 1.7, 1.9)$ , and again start with a mostly annual population: for  $y = 1, 2, \dots, 5$ ,  $X_{1,y} = 996$ ;  $X_{2,y} = 1$ ;  $X_{3,y} = 1$ ;  $X_{4,y} = 1$ ;  $X_{5,y} = 1$ . We assume symmetry across cohorts: for  $\tau \geq 2$ ,  $N_{\tau,5} = N_{\tau,5-1} = \dots = N_{\tau,5-\tau+1}$ . Again, this assumption is not crucial to the possibility of multi-year synchronization in the model;

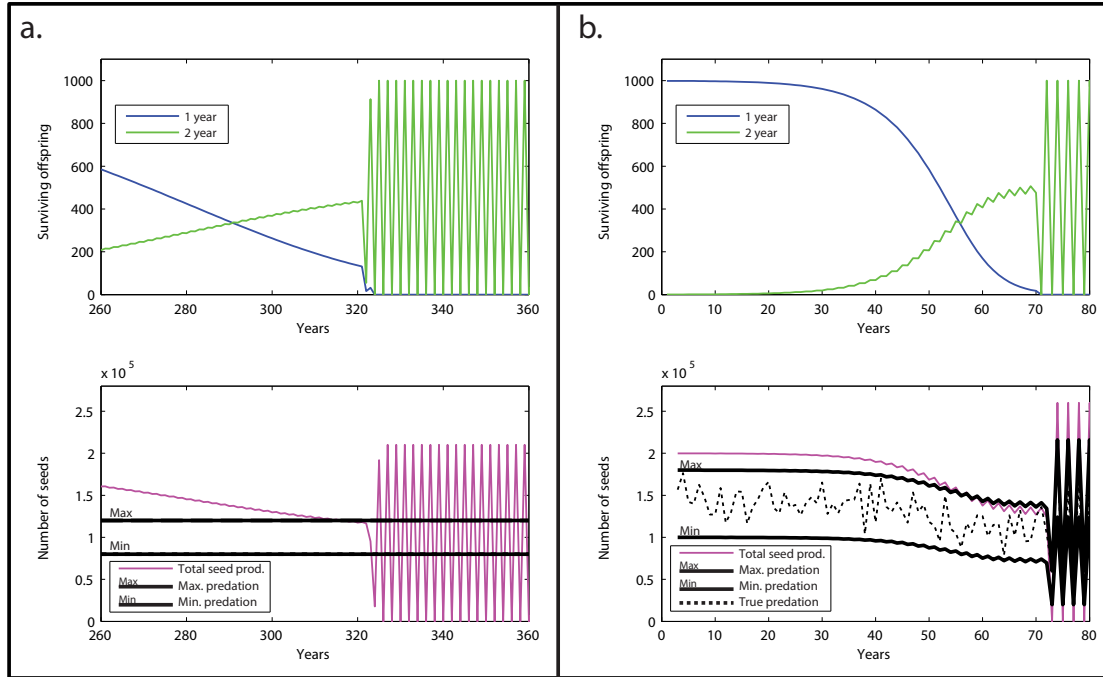


Figure S2: Robustness of the two-year synchronization model. **a.** In the two-year synchronization model, if two-year plants do not release many more seeds than one-year plants, then synchronization onto a two year cycle takes longer. Here, we have assumed that two-year plants release only 5% more seeds than one year plants ( $f_2 = 1.05$ ), and have set minimum and maximum predation rates at  $\alpha = 40\%$  and  $\bar{\alpha} = 60\%$  of the total seed release of an all-annual population. **b.** We can incorporate density-dependent predation rates into the two-year synchronization model, and still observe synchronization onto a two year cycle. Here  $f_2 = 1.3$ , and each year, a baseline predation rate  $\alpha_b$  is drawn randomly from  $[0.1, 0.3]$ , and a density-dependent rate  $\alpha_d$  from  $[0.4, 0.6]$ ; the total possible predation for that year is then calculated as  $\alpha_b KS + \alpha_d S_y$ , where  $KS = 1000S$  is the total seed release of an all-annual population, and  $S_y$  is the true seed release of the population in year  $y$ .

initial asymmetries tend to promote synchronization onto the cycles of initially larger cohorts.

Annual plants release  $S = 200$  seeds each, and here we assume predation again to be significant, independently and uniformly distributed each year between 30% and 70% of the seed release of a full population of annual plants:  $\underline{\alpha} = 0.3, \bar{\alpha} = 0.5$ . Again, distributing predation across narrower or wider intervals preserves the results of the model, although specifying predation as high as for the two-year synchronization model tends to result in total extinction in the current multi-year specification. This is because, as higher-interval plants account for an increasing proportion of the population in this model, seeding becomes even more spread out across years than in the two-year synchronization model, and so lower levels of predation can kill off the entire population than in the two-year model.

Under this specification, synchronization onto a multi-year interval occurs in approximately 62% of simulations. Synchronization occurs onto a single cohort's cycle in roughly 46% of simulations; the remainder of synchronization occurrences are onto two cohorts' cycles (e.g., cohorts 2 and 4 of the four-year plants). Extinction of the entire population is the result in the remaining 38% of simulations.

Of the single-cohort synchronizations, approximately 14% were onto a three year interval, 28% onto a four year interval, and 58% onto a five year interval. No simulations were observed to result in synchronization onto a two year interval.

The rationale underlying synchronization in this model is similar to that for the two-year model. As multi-year plants increase in numbers in the populations (owing to their higher individual seed release), the population's seed release becomes increasingly spread over multiple cohorts, and so annual seed release declines. Once it declines below the maximum possible predation rate, successive eliminations of cohorts can occur, leaving (under this specification) either zero, one, or two cohorts.



## S2 Noise in flowering interval estimates

The broad implication of our model is that the extended mast intervals exhibited by bamboos have evolved through successive multiplications of intervals on which synchronization initially occurred. This in itself does not yet yield a hypothesis that distinguishes the model from other hypotheses for interval growth, since any observed multi-year interval could be factorized into integers which are claimed to be the multiples through which evolution of the interval occurred. That is, any set of observed/measured mast intervals, measured in integer years, could be consistent with our hypothesis.

However, a distinguishing implication can be derived if we introduce the simple, plausible assumption that small multiples in our model would be more likely than large multiples. This would be true if a more complicated, rarer mutation were required to immediately increase flowering time to, say, eleven-fold one's parent's flowering interval than to double it. This seems a reasonable assumption, though, as we have stressed in the main text, the molecular genetics of the biological clock underlying flowering time in masting bamboos are still poorly understood (Nadgauda et al., 1990). It would also be true if, even allowing for the possibility of a mutant with an eleven-fold flowering interval of its parent's, the rest of the genome was not able to cope with such a rapidly and dramatically extended lifecycle. We do not expect the genetics of vegetative construction and maintenance, for example, to be the same as that for flowering time; massive changes in the latter would likely find the former 'unprepared'.

If, then, we restrict our attention to the evolution of extended mast intervals by successive *small* multiplications of an initial synchronization interval, a prediction of the model is that the mast intervals observed today should factorize back into these small multiples and the initial synchronization interval, and as an implication, should factorize into *small primes*.

That is not to say that we can test the hypothesis by simply observing flowering intervals and checking that they strictly factorize into small primes. Variation in measured intervals needs to be accommodated; it can occur for a number of reasons:

- *Timing of observations in mast episodes:* Mast episodes can, for some species, last several years (Janzen, 1976; Kelly, 1994). To calculate the true mast interval, we require flowering observations to be made at precisely the same stage within successive masts. This is unlikely to be the typical case with our data (or any data of this sort). If a flowering observation is reported at the beginning of one such mast episode, and another is reported at the end of the next mast episode, then our estimate of the mast interval will be higher than the true interval. If vice versa, our estimate will be lower than the true interval.

For example, the data in Janzen (1976), which we use here, record two mast episodes for *Phyllostachys bambusoides* in China in 999 C.E. and 1114 C.E. From

the rest of the observations for this species, made much later in Japan, we know that it typically experiences multi-year masts. Thus, we know that the observations made in China record only a stage of the masts in which they occurred. Without knowing the stage within each mast, we cannot know what the exact mast interval was, and thus our estimate of 115 years (1114 – 999) from the two Chinese observations is likely to be imprecise.

- *Location of observations in mast episodes:* Geographically separated populations of the same species are not under selective pressure to maintain synchrony with each other, and so their mast times might differ. Even for a geographically contiguous but large population, mast ‘waves’ have been observed, so that the precise flowering time differs for plants far apart in the population at opposite ends of the wave (Franklin, 2004). To calculate the true mast interval, we would ideally require observations in successive masts from exactly the same small region.

Again, this will often not be the case in the data. For example, Janzen (1976) records two flowering observations for *Chusquea ramosissima* in 1893 and 1916, with the most precise geographic location for both observations reported simply as ‘Brazil’. It is possible that these observations are from the same small region, but it is also possible that the observations were made far apart in Brazil. Without knowing this, we must allow for the possibility that our estimate of a 23 year interval between the masts is imprecise.

- *Recording of aberrant flowering:* In some cases, a small number of plants in a population might flower and set seed out of synch with the rest of the population. A naturalist might correctly record this as an instance of flowering in that species, but not record that it was not a mast. Not being a mast, of course, it is of no use in calculating the mean inter-mast interval of that species. Without being able to discern this in the data, we include it, and it adds noise to our final estimate of the mast interval of the species.
- *Natural variation in the mast interval:* Though a species may be characterized by a clear mean mast interval, there may be slight natural variation in the interval from mast to mast. With enough observations, we may accurately calculate the mean mast interval, but with very few observations, accuracy will be lower.

For example, in Janzen (1976), observations of masting in the long-intervalled *Phyllostachys nigra* f. *henonis* suggest intervals of 59, 63, 60, and 62 years. This variation may be a result of the issues mentioned here in the first two bullet points, or it may reflect natural variation around the well-known mean interval of 60 years in this species.

Accepting that there will be noise in the measurement of mast intervals, our hypothesis predicts they should be *clustered around* numbers that factorize into small primes ('NFSP' hereafter).

It is important to note that the claim that larger multiples are possible is not a counterargument to our model. To see why, we should distinguish clearly between the model we propose—one of interval growth through *any* multiples—and the plausible assumption we have had to make to render the hypothesis testable—that these multiples will usually be small. Countering that large multiples are also possible *assumes* the mechanism that we propose, and is therefore not a counterargument against it. Whatever the case, since the data strongly support our hypothesis (see Section S3), they also implicitly support our assumption that small multiples are more likely.

## S3 Statistical testing

In this section, we present the formulation and results of the statistical methodology we use to test our hypothesis that mast intervals have evolved through successive multiplication, by small factors, of an initial interval. We first present the mast interval data, with a detailed description of the process by which the final data set was reached. We provide an informal assessment of our mast interval data, and discuss the patterns in them that are suggestive of our model of interval multiplication. We then turn to a discussion of exactly what hypothesis should be tested, given the data issues mentioned in the previous section. We then describe the development of a nonparametric approach for testing this hypothesis against an appropriate null hypothesis, the construction of which we also discuss in detail. We then provide the baseline results of this testing, which provides strong evidence for our hypothesis. Finally, we show that these results are robust to many changes in the setup, including the precise hypothesis that we test, the construction of the null, and alterations of the underlying data.

### S3.1 The data

The raw data used are those assembled by Janzen (1976), presented therein as Table 1. This is, to our knowledge, the largest systematic collection of bamboo flowering observations published to date. Additions to it from more modern observations might be possible, though without clear knowledge of Janzen’s criteria for admission and omission, we risk introducing additional sources of noise to Janzen’s data set. For this reason, and for the reason that the original data is adequate for our purposes, we do not add to Janzen’s data set.

Janzen’s data set contains flowering dates (years) for 42 species of bamboo, representing most subtribes within the subfamily. For some species in the data set, flowering intervals, approximate or exact, can be determined from these observations. For some species, however, only very vague conclusions can be made about flowering intervals (e.g., ‘greater than 60 [years], probably greater than 100’ for *Phyllostachys reticulata*). We necessarily exclude such species from our data. For other species, though flowering appears to take place at multi-year intervals, no evidence of a *regular* interval can be discerned from the data. This may be for a number of reasons: issues with measurement such as those described in Section S2, or perhaps true irregularity in those particular species’ flowering patterns. Whatever the case, these species were necessarily excluded from our final data set.

In updating species names to modern usage, we discovered observations for two species listed separately in Janzen (1976), named there as *Arundinaria spathiflora* and *Thamnocalamus spathiflorus*, that are in fact one species with the currently-accepted name *Thamnocalamus spathiflorus*. The observations listed by Janzen under the name



*Arundinaria spathiflora* represent an estimated seven intervals across a span of 71.5 years, at an average (rounded) interval of 10 years (see Table S2). On the other hand, only two observations are listed under *Thamnocalamus spathiflorus*, geographically separate from those listed under *Arundinaria spathiflora*, and representing either one or two intervals (unknown) across 16-17 years. For some reason, Janzen appends a question mark to his estimate of a 16-17 year flowering interval here. Since the estimates are inconsistent across the two listings, and since we have more observations across a greater number of intervals listed under *Arundinaria spathiflora*, and since there is uncertainty both in the number of intervals represented by the observations listed under *Thamnocalamus spathiflorus* and in Janzen's estimate of the mast interval from these observations, we choose to include the observations listed under *Arundinaria spathiflora* in estimating a mast interval for this species.

Finally, we excluded species for which our estimate of mean flowering interval is lower than 10 years – these species we do not consider to exhibit long-intervalled masting. The species omitted by these criteria are listed in Table S1.

Table S1: Species listed in Janzen (1976) that are omitted in our data, and reasons for these omissions. For ease of reference with his data, we first report the species names as they appear in Janzen (1976), followed by updated species names. Regions, observations, and intervals are as reported by Janzen.

Species name (Janzen)	Species name (updated)	Regions	Observations	Intervals (yrs)	Reason for omission
<i>Arundinaria alpina</i>	<i>Yushania alpina</i>	Kenya	?	about 40-plus	No dates reported; interval measure vague.
<i>Arundinaria maling</i>	<i>Yushania maling</i>	Eastern Himalaya	not in living memory 1951	50-plus	Only one date reported; interval measure vague.
<i>Bambusa indusager</i>	?	Paraguay	1972	long interval	Only one date reported; interval measure vague.
<i>Bambusa polymorpha</i>	<i>Bambusa polymorpha</i>	Burma	? 1853	at least 68 at least 50	No clear evidence of regular interval.
		Prome Division Burma	1859-1860 1914	54-55	
<i>Bambusa vulgaris</i>	<i>Bambusa vulgaris</i>	Pantropical	?	150 years plus	No dates reported; interval measure vague.
<i>Chimnobambusa quadrangulus</i>	<i>Chimnobambusa quadrangulus</i>	Japan and Europe, in cultivation	?	greater than 100	No dates reported; interval measure vague.
<i>Chusquea culeou</i>	<i>Chusquea culeou</i>	Chile	?	15-20	No dates reported.

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Table S1 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Intervals (yrs)	Reason for omission
<i>Chusquea quila</i>	<i>Chusquea quila</i>	Chile	?	15-20	No dates reported.
<i>Dendrocalamus giganteus</i>	<i>Dendrocalamus giganteus</i>	Burma-Ceylon (introduced)	1831? 1908-plus	about 76	Uncertainty in dates
<i>Dendrocalamus hamiltonii</i>	<i>Dendrocalamus hamiltonii</i>	Lakhimpur Forest, Assam	1905	30?	No clear evidence of regular interval.
		Cachar, Assam	1912 1956	44	
<i>Dendrocalamus strictus</i>	<i>Dendrocalamus strictus</i>	Gahrwal, outer Himalayan tract	1872-1876 1909-1913	36-40	No clear evidence of regular interval.
		Madhya Pradesh	?	20-30	
		Paniali	1909 1948	39	
		Cachar Hills, Assam	1879 1922 1966	43 44	
		India	1921-1922 1968	46	

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Table S1 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Intervals (yrs)	Reason for omission
		Saharanpur Siwaliks	1883-1886 1926-1927	40-44	
		Bhadravathi, Mysore State	1905-1908 1932-1933	24-28	
		Uttar Pradesh	1870 1909-1910 1949-1953	39-40 39-44	
		Taiwan (introduced)	1922 1969	47	
		Burma:			
		Tharawaddy	none reported	23	
		Zigon	none reported	15, 27	
		Ruby mines	none reported	9	
		Thayetmyo	none reported	21	
		Henzada	none reported	32	
		Prome	none reported	12-15	
		Tauguin	none reported	8	
		Central Provinces:			
		Chanda	none reported	21	
		Seoni	none reported	22	
		Balaghat	none reported	20	

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Table S1 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Intervals (yrs)	Reason for omission
		Madras: Vizagapatam	none reported	28	
		United Provinces: Garwhal Outer Himalayas	none reported	36	
		Saharanpur Siwaliks	none reported	40	
<i>Melocanna bambusoides</i>	<i>Melocanna baccifera</i>	Mizo Hills, Assam	1863-1866 1892-1893 1900-1902 1933 1960	26-30 7-10 31-33 27	No clear evidence of regular interval.
		Lushai Hills, Assam	1864 1911-1912	47-48	
		Chittagong, East Pakistan	1863-1866 1908-1912 1958-1959	42-49 46-51	
<i>Merostachys fistulosa</i>	<i>Merostachys fistulosa</i>	Brazil	?	30-34	No dates reported.
<i>Merostachys</i> sp.	?	Brazil	?	11	No species, dates reported.
<i>Ochlandra travancorica</i>	<i>Ochlandra travancorica</i>	Travancore	1875 1882	7	Interval too short.

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Table S1 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Intervals (yrs)	Reason for omission
<i>Phyllostacys edulis</i>	<i>Phyllostacys edulis</i>	Japan	?	greater than 48	No dates reported; interval measure vague.
<i>Phyllostachys reticulata</i>	<i>Phyllostachys reticulata</i>	Japan	?	greater than 60, probably greater than 100	No dates reported; interval measure vague.
<i>Sasa tessellata</i>	<i>Indocalamus tessellatus</i>	Japan, in cultivation	?	greater than 115	No dates reported; interval measure vague.
<i>Schizostachyum elegantissimum</i>	<i>Nastus elegantissimus</i>	Bandong, Java	?	3	No dates reported; interval too short.
<i>Thamnocalamus spathiflorus</i>	<i>Thamnocalamus spathiflorus</i>	Jaunsar-Bawar, Northwestern Provinces	1865-1866 1882	16-17?	Uncertain estimate; inconsistent with data listed under <i>Arundinaria spathiflora</i> (same species).

Thus, the species that we include are those that are seen in Janzen’s data to exhibit regular, or nearly regular, flowering intervals within a defined region (we do not calculate intervals from observations from different regions, since we do not expect geographically disparate populations to maintain perfect synchrony with each other over long periods of time). Flowering observations for such species often span more than one year (e.g., ‘1875-1876’), which is expected since mast episodes of long-lived bamboos often span multiple years (Janzen, 1976; Kelly, 1994). The process by which we determine the mean flowering interval for each of these species is described below.

For observations of a mast episode over a number of years, we take the midpoint of the observations. So an observation for 1875-1876 is treated as 1875.5.

For cases where there are multiple observations, and they do not suggest a precisely regular interval, we take the earliest and latest midpoint observations for a region, and divide by the number of masts to obtain the average mast interval for that region. This is equivalent to calculating the individual midpoint-to-midpoint intervals for a region and averaging them thereafter (since  $\frac{(t_2-t_1)+(t_3-t_2)+\dots+(t_{n+1}-t_n)}{n} = \frac{t_{n+1}-t_1}{n}$ ). Occasionally, the number of intervals between two observations must be inferred under the assumption that intervals are roughly constant. For example, if a species was observed to mast in 1850, 1860, 1870 and 1890, we infer that there was an unobserved mast around 1880, and that the total number of mast intervals is therefore 4 (i.e., between 5 mast episodes).

If observations exist for multiple regions, we carry out the above procedure for each region, and average across regions, weighting by the number of observed intervals per region.

Final mast interval estimates are rounded to the nearest whole number. Halves are rounded upwards, as per convention.

So, for example, in the case of *Arundinaria falconeri*, introduced to England from the Himalaya, the mast observations are for dates 1847, 1875-1877, 1902-1908, 1929-1932, 1964-1967. We note that there are four mast intervals of roughly 30 years each, and thus include this species in our data, since it appears to exhibit roughly constant mast intervals. We find the midpoints of the observation periods: 1847, 1876, 1905, 1930.5, 1965.5. These imply intervals of 29, 29, 25.5, 35 years respectively. To get the final estimate, we note that the four intervals span  $1965.5 - 1847 = 118.5$  years, at an average of  $118.5/4 = 29.625$  years per interval. This we round to 30 years, which is the final estimate that we include in our data.

Only in cases where a flowering interval is well known and there is significant variation in the Janzen intervals (leading to an estimate that differs from the well-known interval) do we impute the well-known interval value instead of carrying out the above calculations. This we do for three species: (i) *Bambusa bambos*, where the Janzen data includes many observations consistent with the well-known 32 year interval, as well as some much longer  $\sim 40$ -50 year intervals. Including only the observations consistent with a  $< 40$  year

interval, our methodology yields an estimated flowering interval of 31.71 years, which rounds to the known 32 year interval. (ii) *Phyllostachys bambusoides*, where Janzen lists two ancient data points for China suggesting an interval of 115 years, and three more recent observations in Japan, beginning  $602 = 5 \times 120.4$  years after the last Chinese observation, and themselves documenting intervals (midpoint to midpoint) of 120 years and 122 years. Here, we use the well-known 120 year interval. (iii) *Phyllostachys nigra* f. *henonis*, where the well-known interval of 60 years is nearly matched by the Janzen data, which yield a 60.83 year estimate. Excluding the isolated ancient data (first millennium C.E.; last such observation  $> 300$  years before next observation), we get an estimate of 60.09 years, which accords almost perfectly with the well-known 60 year cycle.

The resulting estimates of mast intervals are displayed in Table 1 in the main text. The details of their derivation are given in Table S2.



Table S2: Details of the application of our procedure of mast interval calculation from the data in Janzen (1976). For ease of reference with his data, we first report the species names as they appear in Janzen (1976), followed by updated species names. Regions are as reported by Janzen. The three observations for which we have imputed well-known intervals in place of those that would be estimated from Janzen's data are marked with a star (\*).

Species name (Janzen)	Species name (updated)	Regions	Observations	Midpoints	Average interval (yrs)	Rounded
<i>Arundinaria falcata</i>	<i>Drepanostachyum falcatum</i>	Lansdowne, U.P.	1911 1946	1911 1946	(1946 – 1911)/1 = 35.00	35
<i>Arundinaria falconeri</i>	<i>Himalayacalamus falconeri</i>	England (introduced from Himalaya)	1847 1875-1877 1902-1908 1929-1932 1964-1967	1847 1876 1905 1930.5 1965.5	(1965.5 – 1847)/4 = 29.63	30
<i>Arundinaria intermedia</i>	<i>Drepanostachyum intermedium</i>	Eastern Himalaya	1848 1868 1879	1848 1868 1879	(1879 – 1848)/3 = 10.33	10
<i>Arundinaria racemosa</i>	<i>Sarocalamus racemosus</i>	Sikkim	1857 1888	1857 1888	(1888 – 1857)/1 = 31.00	31
<i>Arundinaria simonii</i>	<i>Pleiolblastus simonii</i>	England (introduced)	1877 1907	1877 1907	(1907 – 1877)/1 = 30.00	30
<i>Arundinaria spathiflora</i>	<i>Thamnocalamus spathiflorus</i>	Western Himalaya	1821 1881-1882 1892-1893	1821 1881.5 1892.5	(1892.5 – 1821)/7 = 10.21	10

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Table S2 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Midpoints	Average interval (yrs)	Rounded
<i>Bambusa arundinacea</i>	<i>Bambusa bambos</i>	Malabar, South	1804	1804	(1866 – 1804)/2 = 31.00	32*
		Kanara (Wynaad & Corg)	1836	1836		
			1866	1866		
		Narbudda River	1839	1839	(1870 – 1839)/1 = 31.00	
			1870	1870		
		Kanara	1878	1878	(1912 – 1878)/1 = 34.00	
			1912	1912		
		Dehra Dun	1836	1836	(1926 – 1836)/2 = 45.00	
			1881	1881		
			1926	1926		
		Brazil (introduced)	1804	1804	(1899 – 1804)/3 = 31.67	
			1836	1836		
			1868	1868		
	1899	1899				
Upper Weinganga Valley, Balaghat District	1818	1818	(1867.5 – 1818)/1 = 49.50			
	1865-1870	1867.5				
Dehra Doon	1832	1832	(1882 – 1832)/1 = 50.00			
	1882	1882				
Chandka Range, Puri Forest Division, Orissa	1929?	1929?	(1969 – 1929)/1 = 40.00			
	1969	1969				

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Table S2 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Midpoints	Average interval (yrs)	Rounded
		South Travancore	1816-1817 1869-1870	1816.5 1869.5	(1869.5 – 1816.5)/1 = 53.00	
		Martaban	?	?	32.00	
					Intervals < 40 yrs, and omitting Martaban obs.: (31.00 × 2 + 31.00 × 1 + 34.00 × 1 + 31.67 × 3)/7 = 31.71	
<i>Chusquea abietifolia</i>	<i>Chusquea abietifolia</i>	Jamaica	1884-1886 1918 1948-1949	1885 1918 1948.5	(1948.5 – 1885)/2 = 31.75	32
<i>Chusquea ramosissima</i>	<i>Chusquea ramosissima</i>	Brazil	1893 1916	1893 1916	(1916 – 1893)/1 = 23.00	23
<i>Chusquea tenella</i>	<i>Chusquea tenella</i>	Brazil	1901 1916 1932	1901 1916 1932	(1932 – 1901)/2 = 15.50	16
<i>Dendrocalamus hookerii</i>	<i>Dendrocalamus hookerii</i>	Assam	1850 1967	1850 1967	(1967 – 1850)/1 = 117.00	117
<i>Guadua trinii</i>	<i>Guadua trinii</i>	Argentina	1923 1953	1923 1953	(1953 – 1923)/1 = 30.00	31

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Table S2 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Midpoints	Average interval (yrs)	Rounded
		Brazil	1902 1934	1902 1934	(1934 – 1902)/1 = 32.00  (30.00 + 32.00)/2 = 31.00	
<i>Merostachys anomala</i>	<i>Merostachys multiramea</i>	Brazil	1876 1906	1876 1906	(1906 – 1876)/1 = 30.00	30
<i>Merostachys burchellii</i>	<i>Merostachys clausenii</i>	Brazil	1877 1907	1877 1907	(1907 – 1877)/1 = 30.00	30
<i>Neehouzeaua dullooa</i>	<i>Schizostachyum dullooa</i>	Cachar, Assam	1951-1953 1967-1968	1952 1967.5	(1967.5 – 1952)/1 = 15.50	16
<i>Oxytenanthera abyssinica</i>	<i>Oxytenanthera abyssinica</i>	Malawi	1925-1930 1943	1927.5 1943	(1943 – 1927.5)/1 = 15.50	16
<i>Phyllostachys bambusoides</i>	<i>Phyllostachys bambusoides</i>	China	999 1114	999 1114	(1114 – 999)/1 = 115.00	120*
		Japan (introduced)	1716-1735 1844-1847 1966-1969	1725.5 1845.5 1967.5	(1967.5 – 1725.5)/2 = 121.00  (115 × 1 + 121 × 2)/3 = 119.00	

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Table S2 – continued from previous page

Species name (Janzen)	Species name (updated)	Regions	Observations	Midpoints	Average interval (yrs)	Rounded
<i>Phyllostachys henonis</i>	<i>Phyllostachys nigra</i> f. <i>henonis</i>	Japan (introduced)	813	813	Including ancient data: (1908 – 813)/18 = 60.83	60*
			931	931		
			1247	1247		
			1666	1666	Omitting ancient data: (1908 – 1247)/11 = 60.09	
			1786	1786		
			1848	1848		
			1908	1908		
<i>Phyllostachys aurea</i>	<i>Phyllostachys aurea</i>	Europe (introduced)	1876	1876	(1936 – 1876)/4 = 15.00	15
			1904-1905	1904.5		
			1919-1921	1920		
			1934-1938	1936		
<i>Sinocalamus copelandii</i>	<i>Bambusa copelandii</i>	Northern Shan States, Upper Burma	1896	1896	(1943 – 1896)/1 = 47.00	47
			1943	1943		
<i>Thyrostachys oliverii</i>	<i>Thyrostachys oliverii</i>	In cultivation from Burma	1891	1891	(1939 – 1891)/1 = 48.00	48
			1939	1939		

### S3.2 What are we formally testing?

The problems with measuring mast intervals precisely, mentioned in the Section S2, prevent us from testing our hypothesis in the simplest manner possible: checking that measured mast intervals almost always factorize into primes below a certain small threshold. Errors in measurement of a mast interval might lead to an estimate of a 47 year interval (does not factorize into small primes) when the true interval is in fact 48 years (factorizes into small primes). Alternatively, while the mean mast interval might be 48 years, small endogenous fluctuations around this mean might lead to a single mast interval of 47 years being correctly measured, but incorrectly inferred to be the mean, or typical, interval for that species.

Given this, two hypotheses are natural to test here. The first is that measured mast intervals should be unusually closely clustered (at an appropriate significance level) around numbers that factorize into small primes (NFSP). That is, for each observation in our data set of measured flowering intervals, we calculate the smallest distance to a NFSP, and find the average of this quantity for our sample. If this average is very low, relative to what we would expect under an appropriate null (at standard significance levels), we would conclude that our measured mast intervals are tightly clustered around NFSP, and consider this evidence in favour of our hypothesis.

The calculation of this sample statistic is simple. For example, given a data set of measured flowering intervals (reported as integer years):  $\{31, 32, 60, 67\}$ , defining ‘small primes’ as 2, 3 or 5, we find the NFSP nearest each observation:  $\{30$  (or  $32$ ),  $32, 60, 64\}$ . The distances from the actual observations to these NFSP are  $\{1, 0, 0, 3\}$ , and so the average distance to a NFSP in this data set is  $(1 + 0 + 0 + 3)/4 = 1$ . This value can then be compared to those of samples generated under an appropriate null.

The second hypothesis is that, in our data set of measured mast intervals, NFSP should be more common than we would expect under an appropriate null hypothesis. Here, we simply calculate the proportion of NFSP in our data set, and test if this proportion is larger than we would expect under an appropriate null, at standard significance levels. Finding that NFSP are unusually common in our data set would of course be strong evidence in favour of our hypothesis.

Calculating this statistic is also simple. In the above data set  $\{31, 32, 60, 67\}$ , 32 and 60 factorize into small primes, while 31 and 67 are not. Thus, the proportion  $2/4 = 0.5$  of the data are NFSP; this value can then be compared to those of samples from the null.

### S3.3 Nonparametric testing approach

With these sample statistics defined, it remains only to specify an appropriate null hypothesis, from which we can derive a null distribution.

Our model states that the long mast intervals of bamboos have increased through discrete interval multiplications. The alternative model would posit that interval growth has proceeded gradually, through small increments. Thus, while our model suggests that measured mast intervals should be clustered around discrete lengths (in particular, NFSP), the alternative model of gradual interval growth predicts a much smoother distribution of mast intervals. For example, our hypothesis would consider measured mast intervals of 30 and 32 years (both factorize into primes 5 or less) to be more likely than 31 years (a large prime), while other models of interval growth would not make such a distinction.

The implication of this is that, under the null hypothesis where intervals have not grown by discrete multiples, the distribution of mast intervals should be smooth, without the many local modes predicted by our hypothesis. Our statistical strategy is thus along the following lines:

1. If our data have in fact come from a *smooth* distribution, as the null hypothesis would imply, what would this distribution look like? We estimate such a smooth distribution from our data, and use this estimate as the null distribution.
2. Drawing samples from such a distribution in a Monte Carlo fashion, how are the key sample statistics (average distance to a NFSP; proportion of NFSP) distributed?
3. In particular, what proportion of samples drawn from such a distribution exhibit sample statistics more extreme (in the sense of being tightly clustered around small primes) than those exhibited by our data? These are the  $p$ -values from which our judgments of the evidence in favour of our hypothesis will be derived.

It is important to consider why the choice of a null distribution might alter our conclusions. NFSP become more sparsely distributed higher up the (integer) number line; a null distribution that places too much weight on higher intervals would overestimate the average distance to a NFSP, and underestimate the average proportion of NFSP. This would increase the chance that the values in our data set appear more extremely clustered around NFSP (*in favour of* our hypothesis). On the other hand, a null distribution that places too much weight on small intervals will tend to produce samples artificially clustered around NFSP, making our data appear less clustered around NFSP, and thus biasing the test *against* our hypothesis. For this reason, the choice of the null distribution must be estimated from the data set, and robustness to the original choice of null distribution must be demonstrated. Our results are demonstrated to be robust to changes in our choice of the null distribution (see Section S3.5). In particular, the data will be shown to be significantly more clustered around NFSP than samples taken from even unfairly bottom-heavy null distributions.

The natural approach to generating a null distribution from the data is to apply kernel density estimation. Since the support of our kernel density (possible mast intervals) must be positive, we employ a transformation method to ensure this. In particular, wanting to restrict the support of the kernel density to between 0 and 150 years, we transform the mast intervals  $x_i$  using the transformation  $\ln(x_i/[150 - x_i])$ , and estimate a kernel density of the transformed data using normal (Gaussian) kernels and a bandwidth of 1 (the bandwidth is unitless, since it applies to the transformed data) We then transform the data back to the original support of 0 to 150 years, resulting in our final kernel density estimate.<sup>1</sup>

We restrict our Monte Carlo sampling to the domain 10-140 years, chosen to accord with our definition of long-intervalled masting (10 years or greater), and to bound the support from above appropriately, so that the null distribution does not generate mast intervals much higher than the highest in our sample. This is a conservative approach, since we have no theoretical reason to believe that the distribution, and our sampling from it, should be bounded so close to our highest observed interval (120 yrs). To allow the null distribution to generate intervals much higher than those in our sample would decrease the typical null clustering around NFSP (for the reasons mentioned in the previous paragraph), and increase the chance that our data look relatively more clustered around NFSP.

Kernel density estimation with these parameters yields the estimated distribution displayed in Fig. S3a. Though the choice of kernel bandwidth is essentially arbitrary, scaled bandwidths (again, the bandwidths discussed here and hereafter apply to kernel density estimation on the transformed data, and are therefore unitless – for this reason, we shall refer to them as ‘scaled bandwidths’) larger than 1 tend to generate distributions tightly collapsed on the lower end of the distribution (Fig. S3c), which the data do not suggest. On the other hand, scaled bandwidths smaller than 1 tend to produce distributions with more than one mode (Fig. S3b). Though, under the null hypothesis of gradual interval growth, an interval length distribution with multiple modes might be expected if frequency-dependent selection were operating on sympatric species, or if there were discrete ecological conditions that selected for shorter and longer interval lengths, these are additional explanatory factors, and the most parsimonious expectation would be of a distribution with a single mode. In any case, we shall show our results to be robust to both changes in the bandwidth.

Finally, having constructed a null distribution, we randomly draw samples from it (Monte Carlo sampling), the same size as our data set, and round their entries to whole numbers (since this is the form in which our data appears). We then calculate the proportions of such samples that exhibit: (i) as low, or lower, an average distance to

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<sup>1</sup>This is the methodology employed, for example, by Matlab’s (v. R2011a) `ksdensity` function when the support is restricted to a finite interval.



NFSP than our data set, and (ii) as high, or higher, a proportion of NFSP than our data set. These are the  $p$ -statistics we use to determine the strength of evidence in favour of our hypothesis.

The hypothesis that we are testing is an unusual one, viz., whether a set of numbers is more clustered around NFSP than chance would predict. As a result, the methodology that we use to test it is also nonstandard. Because of this, before we present the results of its application to our mast interval data, it is worth checking that the methodology does not exhibit systematic confirmation bias. That is, we shall apply the methodology to data generated randomly from some smooth distributions (which should show no statistical tendency to be clustered around NFSP), to make sure that the methodology does not spuriously find evidence that these randomly generated data are significantly clustered around NFSP.

Implementing such a test on data sets generated randomly from a uniform distribution on  $[10, 140]$  and rounded to natural numbers (as for the tests carried out on our true data, the kernel density estimates have support  $[0, 150]$  while the Monte Carlo sampling from these densities is restricted to  $[10, 140]$ ), we find that the methodology does not systematically find the data to be more clustered around NFSP than chance would predict (distance test: average  $p \approx 0.47$ ; proportions test: average  $p \approx 0.43$ ). We carry out a similar procedure on (rounded) samples drawn from a log-normal distribution with parameters  $\mu = 3.36$  and  $\sigma = 0.65$  chosen, using Matlab's (v. R2011a) `fitdist` function, so that the distribution provides a good fit to our data. Samples are restricted to reside in  $[10, 140]$ , with the kernel density estimated on support  $[0, 150]$ , and Monte Carlo

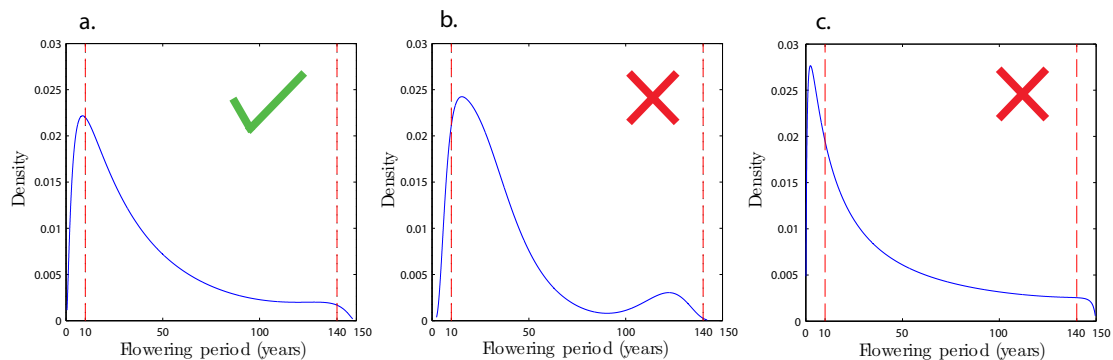


Figure S3: Kernel density estimates of the null distribution, resulting from the null hypothesis of gradual interval growth. Vertical dashed red lines indicate the restricted support, 10-140 years, from which we draw our samples. **a.** The baseline null distribution: Scaled bandwidth = 1.0. **b.** Scaled bandwidth = 0.5, resulting in a bimodal distribution. **c.** Scaled bandwidth = 1.5, resulting in a distribution that places too much weight on small intervals.

samples from the kernel density restricted to  $[10, 140]$ . Again, our methodology does not systematically find that such samples are more clustered around NFSP than chance would predict (distance test: average  $p \approx 0.33$ ; proportions test: average  $p \approx 0.44$ ). Thus, we conclude that our methodology does not suffer from systematic confirmation bias, giving us greater confidence in the results presented in the main text and in Section S3.4.

### S3.4 Test results

#### Distance test

Under the specification above, samples from the null distribution exhibit a mean average distance to NFSP (primes 5 or smaller) of 0.8755. Our data set of mast intervals, on the other hand, exhibits an average distance to NFSP of just 0.3810. This is as low or lower than 99.59% of samples drawn from the null distribution. Thus, by the distance measure, our data are more tightly clustered around NFSP than we would expect under the null hypothesis at significance level  $\mathbf{p} = \mathbf{0.0041}$ . This is a remarkably strong finding given the small sample size, and constitutes powerful evidence in favour of our hypothesis.

#### Proportions tests

Samples drawn from the null distribution contain, on average, 38.79% NFSP (primes 5 or smaller). Our data set of mast intervals, on the other hand, contains fully 71.43% NFSP. This is as high or higher than 99.76% of samples drawn from the null distribution. We thus find that, by the proportions measure, our data set contains a larger number of NFSP than we would expect under the null hypothesis at significance level  $\mathbf{p} = \mathbf{0.0024}$ . Again, this is a very strong result, and is further evidence in favour of our hypothesis.

### S3.5 Robustness of test results

In this section, we demonstrate that our results are robust to many possible changes in the empirical testing. The robustness tests and their results are summarized at the end of this section in Table S3.

#### What numbers should our data be clustered around?

In the baseline specification, the results of which we have reported in Section S3.4, we tested whether our data are significantly clustered around numbers that factorize into small primes, where we define ‘small primes’ as primes 5 or smaller (i.e., 5, 3, and 2). This is an appropriate specification if we believe that initial synchronization would be

unlikely to occur onto an interval greater than 6 years (we cannot distinguish ‘greater than 5’ here, since 6 itself factorizes into small primes 3 and 2), and that mutants with flowering intervals seven-fold (or higher) their population’s mast interval are very unlikely.

Perhaps mutants with flowering intervals five-fold their population’s mast interval are also very unlikely. If we still allow for initial synchronization onto intervals of up to 6 years, but do not allow for subsequent multiples of 5 or higher (with 4 factorizing as  $2 \times 2$ , an interval quadrupling is empirically indistinguishable from two instances of interval doubling), then we should test if our data are significantly clustered around numbers with the following property: the number factorizes into primes 5 or less, but 5 may appear at most once in the factorization (that is, the *multiplicity* of 5 should be one or zero). Maintaining the rest of the properties of the baseline specification, the test of whether our data are significantly clustered around such numbers yields the results reported in column (b) of Table S3. We find very strong evidence that our data are clustered tightly around such numbers (distance test,  $\mathbf{p} = \mathbf{0.0009}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0007}$  respectively). These results are even stronger than in the baseline test.

If we make the stronger restriction that initial synchronization must have occurred on intervals of 4 years or lower, and that subsequent multiples must have been 4 or lower, then we should test whether our data are clustered around NFSP, where ‘small primes’ are taken to be 3 or 2. Maintaining the other properties of our specification, the results of this test are reported in column (c) of Table S3. We do not find evidence that our data are unusually tightly clustered around such numbers (distance test,  $\mathbf{p} = \mathbf{0.6881}$ ; proportions test,  $\mathbf{p} = \mathbf{0.3624}$ ). This might reflect the low power of our statistical methodology given the very small sample size, or it might suggest, given the strong results of the previous tests, that initial synchronization onto intervals of 5 (or more) years has been common in bamboos.

If we make the even stronger restriction that initial synchronization must have occurred onto intervals of at most 2 years, and that intervals could subsequently at most double, then we should test whether our data are significantly clustered around NFSP, where ‘small primes’ refers only to 2. Maintaining the other properties of our specification, the results of this test are reported in column (d) of Table S3. Here, we do find evidence that our data are tightly clustered around such numbers (distance test,  $\mathbf{p} = \mathbf{0.0137}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0100}$ ).

We conclude that our results are, for the most part, robust to changes in the numbers the hypothesis predicts our mast interval data should be clustered around.

### **Bandwidth of kernel density estimation**

Here we test if our results are sensitive to changes in the bandwidth used for our ker-

nel density estimation. As shown in Fig. S3a and discussed in Section S3.3, a scaled bandwidth of 1 yields a density estimate that qualitatively accords with what we would expect under the null hypothesis of gradual interval growth. Scaled bandwidths lower than 1 tend to result in multi-modal density estimates (Fig. S3b), which would require additional selective factors to explain. Scaled bandwidths higher than 1 result in densities concentrated around the lowest observations in our sample (Fig. S3c), which is not in accord with the observed prevalence of longer mast intervals. So, our choice of baseline bandwidth is justified. Nonetheless, since its chosen value is somewhat arbitrary, we would like to know if our results are robust to changes in this value.

Decreasing the scaled bandwidth of the kernel density estimation to 0.5, and maintaining the other properties of the baseline specification, our data remain significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0052}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0025}$ ; column (e) of Table S3). Increasing the scaled bandwidth of the kernel density estimation to 1.5, our data remain significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0049}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0050}$ ; column (f) of Table S3).

Further increases in the scaled bandwidth to 2, 3, and 4 result in distributions increasingly collapsed around modes at the lower and upper bounds of the support, with little weight in between. Though these are of course not distributions we would expect under the null hypothesis, our results remain robust to their usage (in all cases, clustering in distance test and proportion test comfortably significant at 5% level – results not reported in Table S3).

Our results are thus robust to changes in the bandwidth used in kernel density estimation.

### Support of kernel density estimation

As noted earlier, over-restricting the support of our density estimation will tend to yield samples from the null distribution with smaller numbers, and since smaller numbers are generally more likely to factorize into small primes than larger numbers, this would tend to make samples from the null look artificially more clustered around NFSP, and our data relatively less so, biasing our statistical testing *against* our hypothesis. On the other hand, under-restricting the support will allow for numbers too large in samples from the null, and will thus tend to bias the testing *in favour* of our hypothesis. We would thus like to know if our results are robust to decreases (especially) and increases in the support of the kernel density estimation of the null distribution.

Decreasing the support of the density estimation to 0-130 years, drawing samples only from the 10-120 years region of the resulting distribution, and otherwise maintaining all the properties of the baseline specification, we still find (column (g) of Table S3) that our data are significantly tightly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0043}$ ;

proportions test,  $\mathbf{p} = \mathbf{0.0023}$ ). This is reassuring, since we can be confident that a drawing support of 10-120 years is unfairly over-restrictive, given that two observations in our data set are right up against its upper bound.

Increasing the support of the density estimation to 0-170 years, drawing samples only from the 10-160 years region of the resulting distribution, and otherwise maintaining all the properties of the baseline specification, we still find (column (h) of Table S3) that our data are significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0038}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0019}$ ).

Thus, our results are robust to changes in the support on which the kernel density estimate of the null distribution is made.

### **Kernel type in kernel density estimation**

In our baseline kernel density estimation, we used normal (Gaussian) kernels. This yielded a kernel density estimate that was qualitatively consistent with the null distribution we would expect under the null hypothesis of gradual interval growth. Nonetheless, it would be reassuring if our results were robust to the usage of other kernel types.

Using Epanechnikov kernels, and otherwise maintaining all the properties of the baseline specification, we still find (column (i) of Table S3) that our data are significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0050}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0033}$ ).

Using triangular kernels, and otherwise maintaining all the properties of the baseline specification, we still find (column (j) of Table S3) that our data are significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0047}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0030}$ ).

Our results are thus robust to the choice of kernel in the kernel density estimation of the null distribution.

### **Changes in the data**

As noted in Section S3.1, we deviated from the regular methodology used to calculate mean mast intervals from flowering observations reported in Janzen (1976) in two instances (for three species).

First, we imputed the well-known intervals of 60 years and 120 years for *Phyllostachys nigra* f. *henonis* and *P. bambusoides* respectively, though the data from Janzen resulted in estimates of 61 years and 119 years respectively. These changes are justified for several reasons: In the case of *P. nigra* f. *henonis*, excluding isolated ancient observations (first millennium C.E., last such observation more than 300 years before next observation in Janzen's data) results in an estimate that is very close to the well-known 60 year interval of this species (60.09 years). In the case of *P. bambusoides*, regional variation in the estimates of this species' mast interval results in significant uncertainty in our

estimate by standard methodology, and we prefer to impute the well-known 120 year cycle.

Second, our methodology would lead us to discard *Bambusa bambos* from our data, despite its known 32 year mast interval having been well documented (see, e.g., Seifríz, 1923). The flowering observations in Janzen (1976) are, for many regions, consistent with the known 32 year interval. For other regions, though, much longer intervals ( $> 40$  years) are reported, with much variation. If we restrict attention to the observations consistent with a mast interval less than 40 years, our methodology results in an estimated mast interval of 31.71 years, which rounds to 32 years, the well-known mean interval of this species. As a result, we are justified in including the well-known 32 year interval of this species.

These changes are thus well justified. Nonetheless, we would be further reassured if our results could be shown not to rely on them. In column (k) of Table S3, we report the results of our tests, reverting the data points for *P. nigra* f. *henonis* and *P. bambusoides* to 61 years and 119 years respectively, and otherwise maintaining the baseline specification. Here, we still find that our data remain significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0204}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0268}$ ).

In column (l) of Table S3, we report the results of our tests, omitting the data entry for *B. bambos*. We find that our data remain significantly clustered around NFSP (distance test,  $\mathbf{p} = \mathbf{0.0069}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0044}$ ).

Finally, in column (m) of Table S3, we report the results of our tests, reverting the data entries for *P. nigra* f. *henonis* and *P. bambusoides* to 61 years and 119 years respectively, and omitting the data entry for *B. bambos*. Again, we find that our data are significantly clustered around NFSP by the distance test (distance test,  $\mathbf{p} = \mathbf{0.0318}$ ; proportions test,  $\mathbf{p} = \mathbf{0.0455}$ ).

We conclude that, even though the changes made to our data are strongly justified in the first place, our results are largely not sensitive to them.

Table S3: Robustness tests. Baseline specification in column (a). For each test (b)-(m), the change from the baseline specification is in bold font.

	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
	Baseline	Initial synch $\leq 6$ , multiples $\leq 4$	Primes $\leq 3$	Primes $\leq 2$	Bandwidth smaller	Bandwidth larger	Support smaller	Support larger
<i>Cluster around:</i>	NFSP, $\leq 5$	<b>NFSP, <math>\leq 5</math>; multiplicity of factor 5 is <math>\leq 1</math></b>	<b>NFSP, <math>\leq 3</math></b>	<b>NFSP, <math>\leq 2</math></b>	NFSP, $\leq 5$	NFSP, $\leq 5$	NFSP, $\leq 5$	NFSP, $\leq 5$
<i>Kernel density:</i>								
Support for kernel	0-150	0-150	0-150	0-150	0-150	0-150	<b>0-130</b>	<b>0-170</b>
Drawing support	10-140	10-140	10-140	10-140	10-140	10-140	<b>10-120</b>	<b>10-160</b>
Kernel type	Normal	Normal	Normal	Normal	Normal	Normal	Normal	Normal
Scaled andwidth	1.0	1.0	1.0	1.0	<b>0.5</b>	<b>1.5</b>	1.0	1.0
<i>Data used:</i>	All data, corrected	All data, corrected	All data, corrected	All data, corrected	All data, corrected	All data, corrected	All data, corrected	All data, corrected
<b>P</b> <sub>distance</sub>	0.0041	0.0009	0.6881	0.0137	0.0052	0.0049	0.0043	0.0038
<b>P</b> <sub>proportions</sub>	0.0024	0.0007	0.3624	0.0100	0.0025	0.0050	0.0023	0.0019

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Table S3 – continued from previous page

	(i)	(j)	(k)	(l)	(m)
	Kernel type 1	Kernel type 2	Data change 1	Data change 2	Data change 3
<i>Cluster around:</i>	NFSP, $\leq 5$	NFSP, $\leq 5$	NFSP, $\leq 5$	NFSP, $\leq 5$	NFSP, $\leq 5$
<i>Kernel density:</i>					
Support for kernel	0-150	0-150	0-150	0-150	0-150
Drawing support	10-140	10-140	10-140	10-140	10-140
Kernel type	<b>Epanechnikov</b>	<b>Triangle</b>	Normal	Normal	Normal
Scaled bandwidth	1.0	1.0	1.0	1.0	1.0
<i>Data used:</i>	All data corrected	All data, corrected	<b><i>P. nig. f. h. 61;</i></b> <b><i>P. bamb. 119</i></b>	<b>Without <i>B. bamb.</i></b>	<b>Without <i>B. bamb.</i>;</b> <b><i>P. nig. f. h. 61;</i></b> <b><i>P. bamb. 119</i></b>
<b>p</b> <sub>distance</sub>	0.0050	0.0047	0.0204	0.0069	0.0318
<b>p</b> <sub>proportions</sub>	0.0033	0.0030	0.0268	0.0044	0.0455



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