

## LETTER

# Extended flowering intervals of bamboos evolved by discrete multiplication

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### 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).

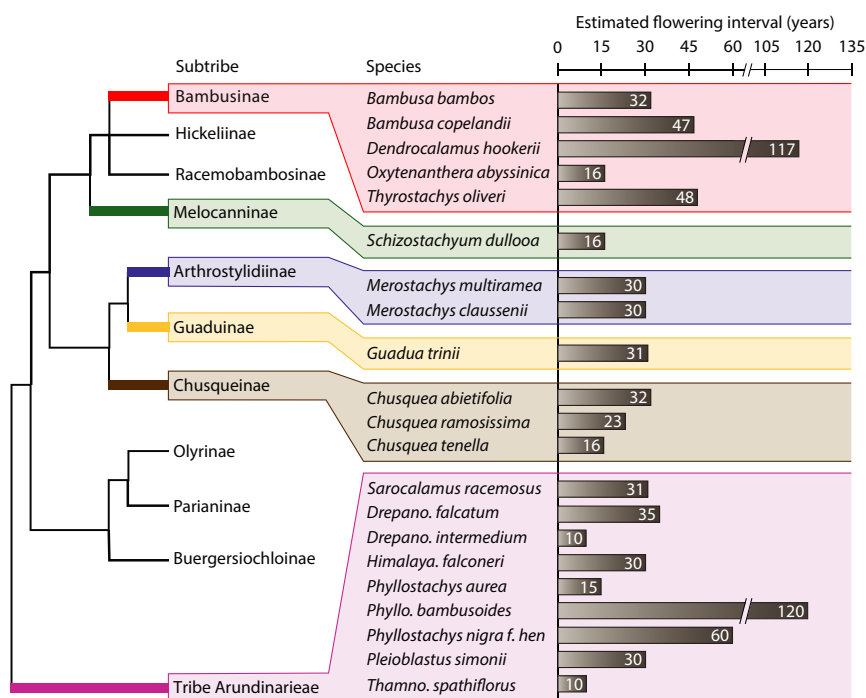
A third explanation, the so-called fire cycle hypothesis (Keeley & Bond 1999), argues that the large seed release

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**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

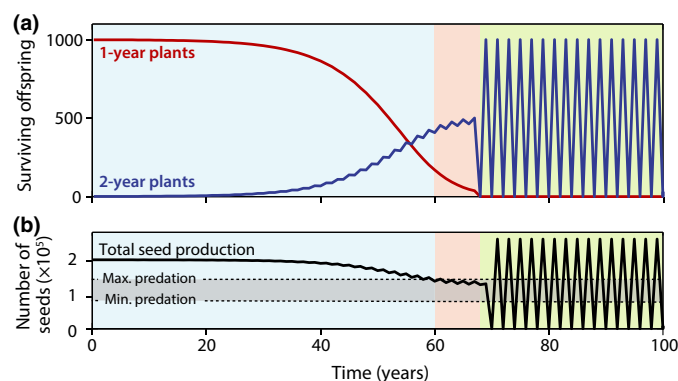
Once synchronisation has been established in a population, say, on a 3-year mast interval, stabilising selection should maintain synchrony. This is because a plant flowering out of sync – for example, after 2 or 4 years – would release its seeds alone, and thus have its entire seed set consumed by predators. 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

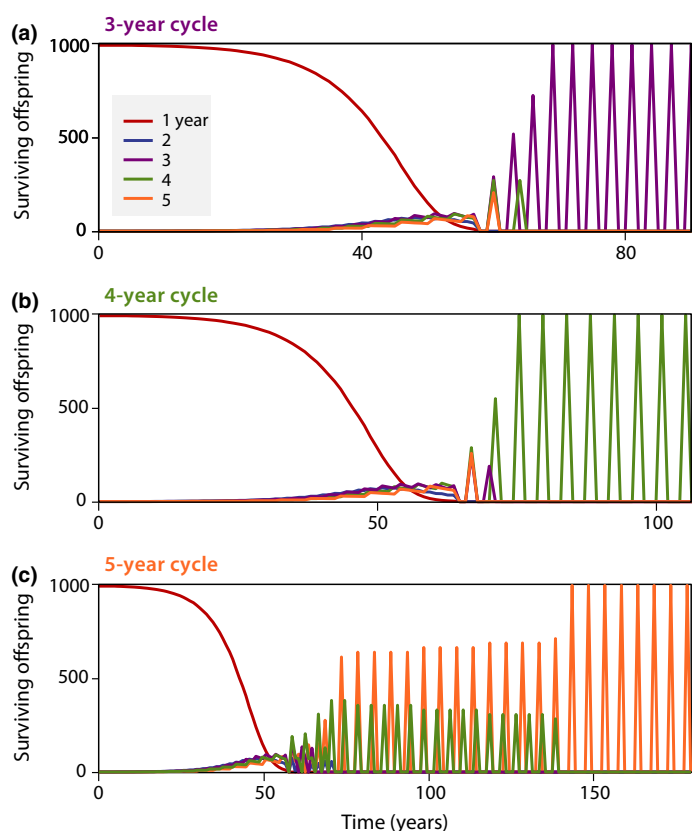
flowering period increases to a multiple of its initial synchronisation interval.

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.

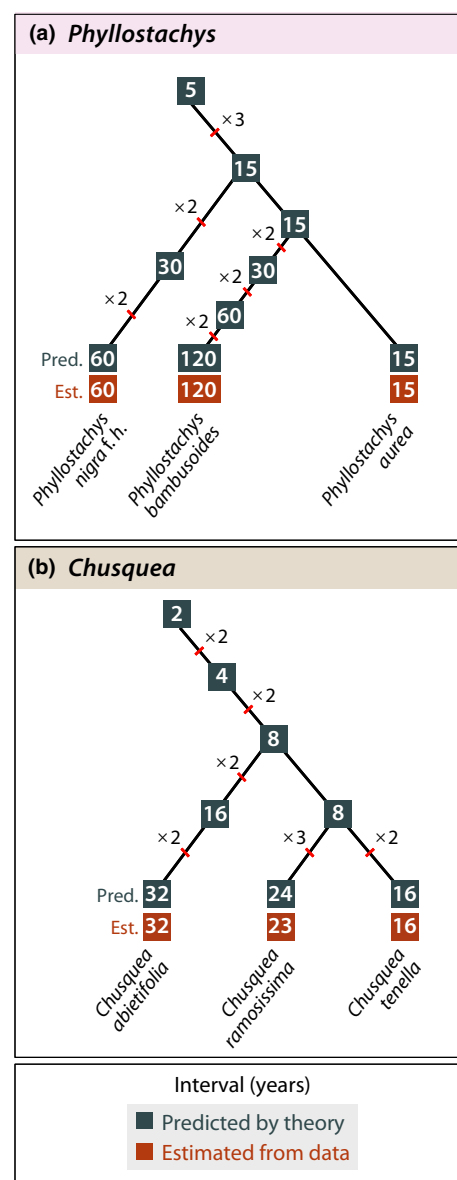
Nonetheless, a broader inspection of the estimated mast intervals of these less well-studied species, together with their phylogenetic placement, corroborates our hypothesis. In the two monophyletic genera in our data that exhibit variation in mast intervals across more than two species, *Phyllostachys* 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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