



Evolutionary Drivers, Proximate Mechanisms, and Spatial Synchrony of Acorn Production in Oaks

Walter D. Koenig^{1,2}, Mario B. Pesendorfer^{1,2}, and Johannes M. H. Knops³

1. Lab of Ornithology, Cornell University,
159 Sapsucker Woods Road,
Ithaca, NY 14850 USA
wdk4@cornell.edu

2. Hastings Reservation, University of California, Berkeley,
38601 E. Carmel Valley Road, Carmel Valley, CA 93924
USA

3. School of Biological Sciences, University of Nebraska,
348 Manter Hall, Lincoln, NE 68588 USA

ABSTRACT

Masting behavior – the highly variable and synchronized production of seeds by a population of plants – is common among oaks and has dramatic effects on resource dynamics and community structure. Based on the California Acorn Survey, our long-term study of acorn production by California oaks, we summarize the major hypotheses driving this phenomenon along with some of the questions remaining to be answered about masting at both the functional (ultimate) and mechanistic (proximate) levels of analysis. We also discuss one of the key issues regarding the definition of masting, namely what constitutes a population. This latter issue has recently been addressed by quantifying spatial synchrony, the spatial and temporal scale at which acorn production is synchronous. The drivers of spatial synchrony differ dramatically depending on the spatial scale of interest; at the relatively small spatial scale of individual trees a few km apart, the primary drivers for one species we have studied in detail, *Quercus lobata* Née (valley oak) are local environmental factors such as soil nutrients and water availability, whereas at the large spatial scale of several hundred km the drivers of both differences in overall productivity and spatial synchrony are primarily more general environmental factors, specifically weather.

Keywords: California Acorn Survey, economy of scale, masting, Moran effect, pollination efficiency, predator satiation, resource matching

Introduction

Masting or mast-fruiting, the highly variable and synchronized production of seeds by a population of plants, has been recognized for over 250 years (Ellis 1743: “Under these trees, the hogs generally get pork in a maste-year”; cited in the Oxford English Dictionary). It is only much more recently, however, that workers have investigated this enigmatic phenomenon critically and begun to understand both its ecological drivers and evolutionary implications.

One of the earlier evolutionary considerations of mast-fruiting can be found in Stearns (1976), who briefly outlined several hypotheses for mast-fruiting as part of his discussion of life-history adaptations to different kinds of environments. The start of the modern scientific investigation of masting behavior, however, can reasonably be attributed to Silvertown (1980), who was the first to conduct a meta-analysis with the goal of testing the most long-standing and durable evolutionary hypothesis for this phenomenon, the idea that masting behavior increases the survival of seeds by reducing the probability of seed predation (the “predator satiation” hypothesis). Following Silvertown’s review, subsequent papers generally focused on the implications of masting behavior for seed dispersal and seedling survival. This changed with the landmark paper by Norton and Kelly (1988), which analyzed variable seed production by the rimu (*Dacrydium cupressinum* Sol. ex G. Forst.), a New Zealand coniferous tree. Norton and Kelly’s key contribution was to identify alternative hypotheses for masting behavior and to point out that most involved an “economy of scale” such that occasional larger episodes of reproduction are more efficient than more regular, smaller ones.

Hypotheses involving some economy of scale include not only predator satiation but the possibility that a higher proportion of flowers may be successfully fertilized in mast years (the “pollination efficiency” hypothesis) and the hypothesis that masting occurs following events that portend environmental conditions favorable to seedling establishment (the “environmental prediction” hypothesis). The key feature of all economy of scale hypotheses is that they require more from the plants than simply responding to current conditions; in other words, they are an adaptive response to some ecological factor and thus a product of selection. As such, they require an evolved mechanism on the part of the plant to produce the highly variable patterns of reproduction characteristic of this phenomenon.

The senior author’s interest in masting behavior stems from a long-term study, still ongoing, of the acorn woodpecker (*Melanerpes formicivorus* Swainson), a species common in California whose extraordinary social behavior is matched only by its unique habit of individually storing acorns, often by the thousands, in special trees modified by the birds called storage trees or granaries (Photo 1). As part of this study, we noted that almost everything about these birds, from their family-living behavior to their reproductive success, seemed to be dependent on the size of the acorn crop, which varied dramatically from year to year. Oddly, however, there was relatively little information on the factors that drove such variability, and thus we initiated what we now call the California Acorn Survey in autumn of 1980.

The original goal of the California Acorn Survey was to use brief (15 s by each of two observers for a total of 30 s) visual counts of acorns (Koenig et al. 1994a) on marked trees to quantify annual variation in seed production by the various species of oaks at our study site and use the data to gain a greater understanding of the ecological variables

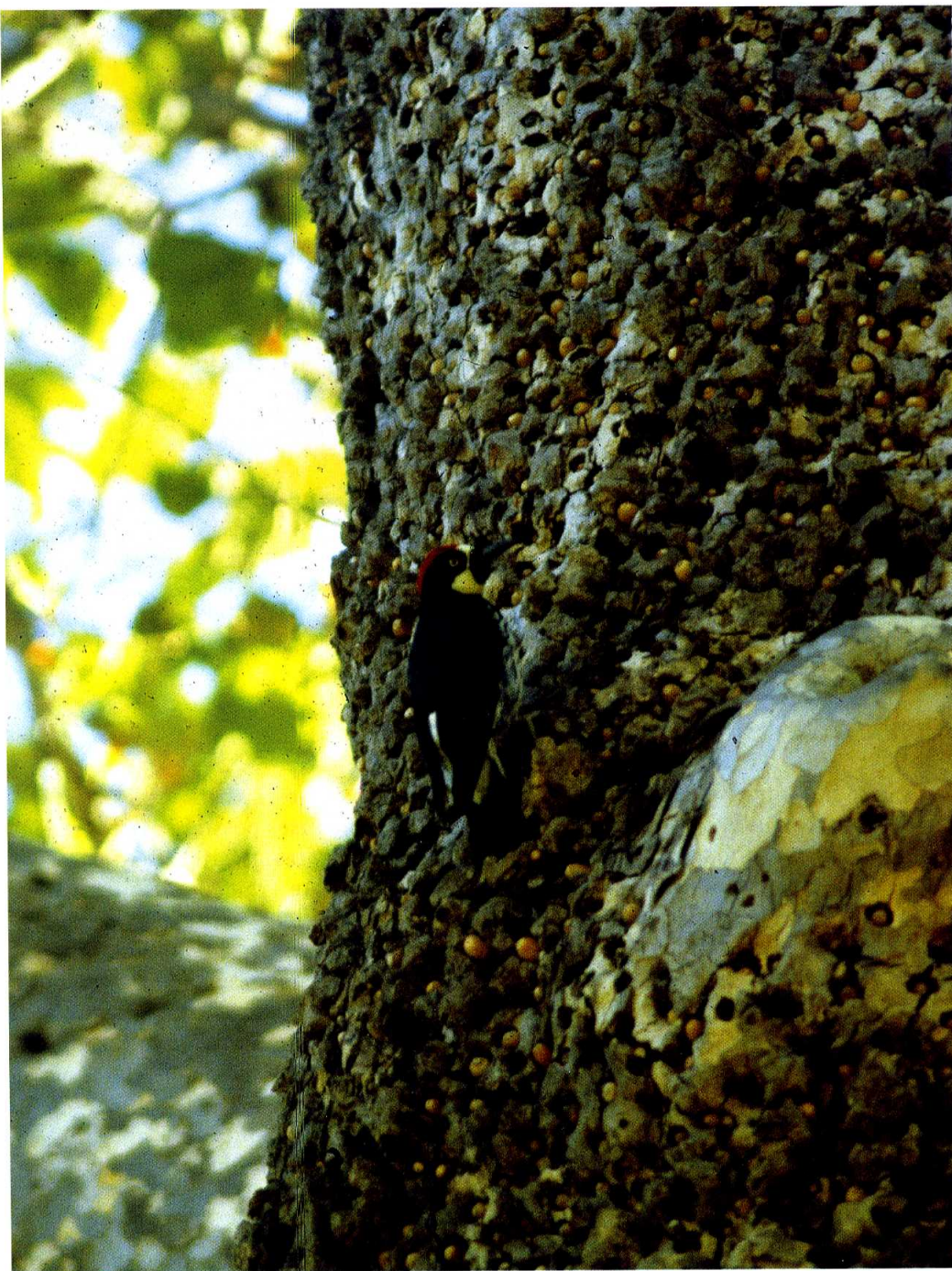


Photo 1/ An acorn woodpecker defending acorns stored in its family's granary, in this case *Platanus racemosa* (California sycamore).

selecting for the unusual social behavior of the birds we were studying. Within a few years, however, the survey took on a life of its own, eventually expanding to encompass mast surveys at 20 sites across the entire state of California and the additional goal of understanding the drivers of variable acorn production at multiple levels of analysis.



Photo 2/ Using binoculars to visually count acorns on the California Acorn Survey.

Here we summarize some recent findings and discuss a few of the problems that remain to be solved before we gain a complete understanding of masting behavior in oaks and other forest trees.

Ultimate drivers

Despite the intuitiveness of the predator satiation hypothesis, there are at least two reasons why it is unlikely to provide the only, and in some cases possibly even the main, selective advantage to masting in oaks. The first is that the main vertebrate predator of acorns, birds in the family Corvidae (jays and magpies) are typically also their main dispersers (Pesendorfer et al. 2016b). As a consequence, the selective advantage of reducing jay populations by means of poor acorn years is counteracted by the selective disadvantage of decimating the primary agents of seed dispersal during good acorn years.

In its most extreme form, predator satiation predicts that all masting species in a community will be selected to produce seed crops that are both highly variable and highly synchronized, thus severely reducing or even eliminating seed predators. In contrast, maintaining healthy seed dispersal agents such as jays is likely to select for asynchronous seed production interspecifically, and possibly even intraspecifically, depending on whether the birds are attracted to groups of trees masting synchronously or individual trees producing large seed crops, and the interactions between different species of seed predators/dispersers (Pesendorfer et al. 2016).

Interestingly, seed production by oak communities often appears to conform more closely to this latter, asynchronous, pattern. This is a consequence of the second reason why predator satiation is unlikely to be the only evolutionary factor selecting for masting: the frequent co-occurrence of species in different sections that typically require a different number of years (one vs. two) to mature acorns (Mohler 1990), and as a result do not mast synchronously (Koenig et al. 1994b). Thus, regardless of how synchronous acorn production by individual species may be, acorn availability on the community level is

generally moderated at any site where oaks of different sections coexist, such as is typically the case in North America and anywhere that oaks in both the White and Red sections are sympatric. On a community level, masting by oaks is not particularly striking.

If masting in oaks is not selected for exclusively by predator satiation, what other factors are important? Counteracting selection for seed dispersal is clearly one important evolutionary factor. For these wind-pollinated, self-incompatible species, another important alternative is that trees are able to achieve more efficient pollination by investing their resources in occasional years of large flower and seed production rather than spreading their resources out across all or most years. This “pollination efficiency” or “pollen coupling” hypothesis assumes that pollen is limited in at least some years, a possibility that has only recently been confirmed in wind-pollinated species (Koenig and Ashley 2003; Koenig et al. 2012; Pearse et al. 2015). Evidence for the importance of the pollination efficiency hypothesis has, however, been accumulating for some time both empirically (Kelly et al. 2001; Knapp et al. 2001; Sork et al. 2002; Moreira et al. 2014) and theoretically (Satake and Iwasa 2000, 2002a, b).

Although evidence that more than one factor plays a role in selecting for masting behavior in oaks exists, quantifying the relative importance of each is difficult and there has as yet been no study that has unambiguously been able to disentangle them. Perhaps the best attempt so far is the conceptual model developed by Kelly et al. (2001), which attempts to quantify the importance of pollination efficiency. Their results suggest that masting can be evolutionarily favored by either one factor or a combination of factors, and that the relative importance of different factors may vary both between and within species depending on variables such as altitude, fragmentation, and plant density. Clearly more work needs to be done to understand the importance of different adaptive hypotheses for masting behavior in oaks and how they are influenced by environmental and ecological factors.

Proximate drivers

Although many gaps regarding the functional (evolutionary) basis of masting remain, we know even less when it comes to the proximate drivers of variable seed production (Crone and Rapp 2014; Pearse et al. 2016). This is most obvious when considering the large literature on the relationships between weather and seed production, both in oaks and other masting species, particularly conifers. Clearly weather correlates with subsequent seed production in many species. But why? How, exactly, do trees “see” different kinds of weather conditions and use them to decide how much to invest in seed production in a particular year?



Photo 3/ *Quercus lobata* (valley oak) on Liebre Mountain in northern Los Angeles County, California.

In many White Oaks (section *Quercus*), for example, warm, dry conditions during the spring generally correlate with large acorn crops the subsequent autumn (Sharp and Sprague 1967; Sork et al. 1993; Koenig et al. 1994b). In our study site in central coastal California, the strongest correlation between weather and the annual acorn crop in valley oaks (*Quercus lobata* Née), is with mean maximum temperature in April (Photos 3 and 4). Since flowering in this population occurs primarily in March and April, these results suggest that weather affects pollen flow and/or fertilization of flowers in this population. But how?

The answer to this question has important implications for issues such as how and if climate change will affect masting behavior. One relatively straightforward possibility is the “pollen wash-out” hypothesis, that cool, wet conditions during flowering directly inhibit pollen flow by washing pollen out of the air (Pérez-Ramos et al. 2010). Another, more complicated possibility is the “phenological synchrony” hypothesis that synchrony of flowering driven by microclimatic variability drives annual differences in pollen availability and pollination success (Koenig et al. 2015)(Figure 1). Despite patterns related to life history and phylogeny, however, the weather factors that correlate with seed production are often different for different species, and thus there are almost certainly other mechanisms potentially linking weather and seed production in masting species (Koenig et al. 2016).

To the extent that seed production is affected by weather through the latter’s effects on pollination success, pollination is potentially important to masting at both the ultimate evolutionary level, via pollen coupling, and proximate mechanistic levels of analysis. It is nonetheless important to try and distinguish these levels and make it clear which one is being considered in any particular analysis.

The pollen wash-out and phenological synchrony hypotheses are predicated on the assumption that weather is a mechanistic driver of masting behavior (Pearse et al. 2014). An alternative, however, is that weather is simply a cue sensed by the trees and perhaps amplified in some way so as to result in variable seed production (Kelly et al. 2013). To the extent that this is true, it is possible that masting will not be influenced by climate change, whereas if weather affects acorn production because of its close mechanistic relationship to acorn production, it is likely that climate change will directly affect masting (Koenig et al. 2015). This is another area that is clearly in need of additional study.

How weather affects acorn production is only one aspect of the issues related to the proximate drivers of masting behavior in oaks. The second major issue is the role of resources. Acorns of most oak species are relatively large and cannot be conjured out of nothing, and thus resources are clearly necessary in order to produce them. Exactly what resources are critical, where they come from, and whether they are limiting or not are all questions that remain to be fully understood.

As pointed out recently by Pearse et al. (2016), there are at least four different ways that resources may play a role in seed production. The first of these, resource matching, is the idea that masting behavior is a response to varying levels of resources that happen to be available from one year to the next. This idea, which dates back to the early part of the 20th century (Büsgen and Münch 1929), is the one hypothesis that does *not* require that masting behavior be the result of an economy of scale nor the product of selection. Studies investigating this hypothesis have generally found that variability in resources that are likely to be involved in masting is much smaller than variability in seed production,

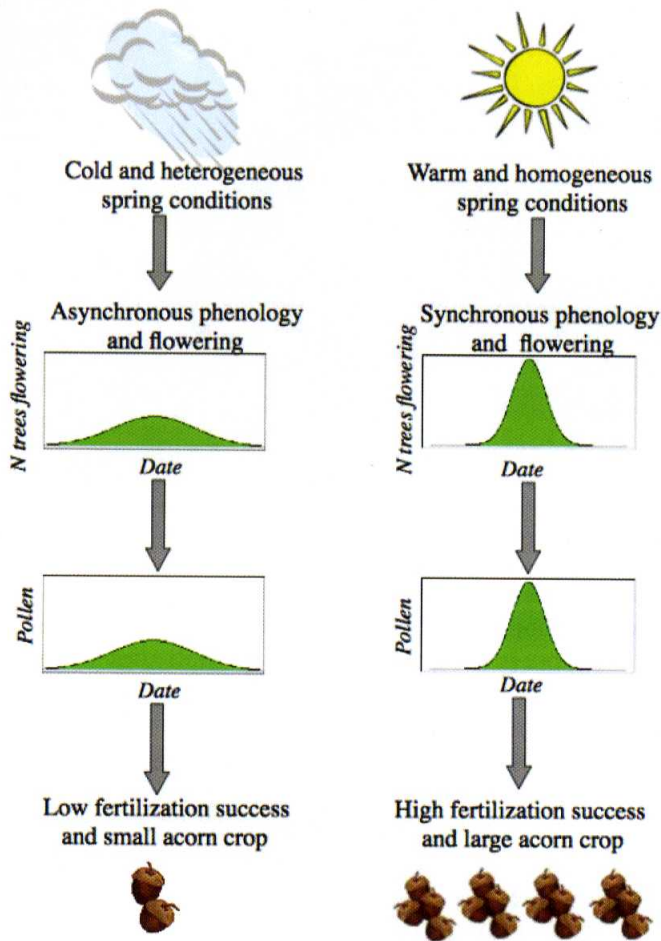


Figure 1/ The phenological synchrony hypothesis, from Koenig et al. (2013). The hypothesis proposes a mechanism for how differences in weather conditions during the spring may interact with synchrony among trees in their flowering phenology to determine the overall size of the subsequent acorn crop.

countering a key prediction of this hypothesis (Koenig and Knops 2000). Also contrary to this hypothesis is the negative temporal autocorrelation in seed production reported in many species; that is, a good mast year is generally followed by a relatively poor one, and vice versa (Sork et al. 1993; Koenig et al. 1994b). In contrast, a positive correlation between growth and reproduction within individuals among years provides support for the resource-tracking hypothesis; this pattern has rarely been observed in masting species, however (Kelly and Sork 2002).

A second way that resources might be important in seed production is if resources are “switched” between reproduction and some other function – most obviously growth – within years. Such a pattern is potentially consistent with resources being relatively consistent from one year to the next, since the greater variability in seed production is hypothesized to be due to differences in the proportion of resources devoted to



Photo 4/ *Quercus douglasii* (blue oak) acorns. A large acorn crop such as this may require use of resources stored up by trees over several years.

reproduction, not differences in resource availability per se. A strong negative correlation between growth and reproduction is consistent with this hypothesis. Such a relationship does occur in many oaks, but is not general and is potentially due to opposite correlations of weather with growth and reproduction rather than to a direct trade-off between these two life-history variables (Knops et al. 2007).

The third potential role of resources is via storage. Resource storage has played a prominent role in thinking about masting behavior ever since publication of the elegant model of Isagi et al. (1997) hypothesizing that mast years entail the expenditure of a large amount of resources that may require several years for the trees to accumulate. Expanding this model has become something of a cottage industry and has resulted in numerous insights as to the potential roles of pollen coupling and weather in masting behavior (Satake and Iwasa 2000, 2002a, b; Abe et al. 2016; Monks et al. 2016; Pesendorfer et al. 2016a).

Unfortunately, there are considerable logistic difficulties in testing these models empirically, and analyses investigating the role of resource storage in masting behavior have thus far yielded conflicting results (Crone and Rapp 2014; Pearse et al. 2016). Among the problems are that we as yet do not know what resources may be critical and the fact that oaks are modular in structure and thus resource storage may occur on a smaller scale than that of the entire tree (Sánchez-Humanes et al. 2011).

The fourth way that resources may play a role in seed production is by what Pearse et al. (2016) refer to as “veto” mechanisms. Basically, the idea is that weather conditions make it impossible for trees to produce as many acorns as they could in any particular year, and that the resources that are “saved” are then either used for other functions (growth, for example), or possibly stored and made available for seed production the next year. Variable seed production then results not because of switching or storage per se (although either or both are potentially involved), but rather because of different levels of effort that the “veto” mechanism allows the tree to expend on reproduction in any one year.

What combination of these models applies to oaks? This problem has yet to be answered. Not only is it likely that different species are dependent on different mechanisms for their patterns of acorn production, but it is also probable that switching, resource storage, and veto mechanisms all play some role in variable acorn production. Determining the relative importance of each is a problem that will require considerable effort, since it is likely to require proximate analyses of potentially key resources both within and among trees across multiple years.

The good news is that there is considerable variability in masting behavior among oaks, and thus that appropriate comparisons will potentially provide considerable insights as to the mechanisms driving observed differences. There is also a relatively similar acorn-producing, but largely insect-pollinated sister groups, the tanoaks (*Notholithocarpus*) and lithocarps (*Lithocarpus*), whose contrast with wind-pollinated *Quercus* species may be uniquely useful for determining the importance of wind pollination to masting behavior. Based on the California Acorn Survey, for example, the (mean) coefficient of variation (CV; a standard measure of masting behavior equal to the standard deviation divided by the mean expressed as a percentage) for three populations of *Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. H. Oh, the California tanoak, is 29.5%, whereas for seven populations of *Q. kelloggii* Newb. (California black oak), a species found in roughly the same habitat that also requires two years to mature acorns, the mean CV is 77.0%, a significant difference (Wilcoxon sign-rank test, $P = 0.02$). This supports the hypothesis that wind pollination plays a key role in producing the highly variable, synchronized reproduction characteristic of oaks. Since wind pollination is likely to be important as a veto mechanism rather than playing any role in resource switching or storage, this difference by itself supports the hypothesis that veto mechanisms are key to the relatively highly variable seed production behavior observed in many oak species.

Even more challenging, but potentially more illuminating, may be experimental studies manipulating resources and seed production, such as have been performed on mast-fruited wildflowers (Crone et al. 2009) and grasses (D. Kelly, unpublished data), but not as yet on oaks. Such manipulations are difficult due to the large size of tree oaks. Many oak species grow in both tree and shrub forms, however, and resource manipulations on the latter offer a potentially important means of inferring what is going on in larger, less tractable forms of this genus.

Spatial synchrony

As mentioned at the start, masting behavior is defined as variable and synchronized reproduction by a population of trees. But how large is that population? One of the more dramatic discoveries of recent studies, both of oaks and of several other taxa, is the remarkably large geographic scale of synchrony in masting behavior. In the case of *Q. lobata*, for example, significant synchrony in acorn production is detectable across their entire geographic range encompassing a distance of over 700 km and millions of individual trees (Koenig and Knops 2013)(Figure 2). What drives such impressive synchrony?

The primary candidates in this case are in some sense the usual suspects: weather – a phenomenon known as the “Moran effect” after the Australian mathematician who first recognized the potential importance of this relationship – and pollen coupling, the dependence of oaks on pollen from other individuals to fertilize their flowers. Spatial

Statewide spatial synchrony

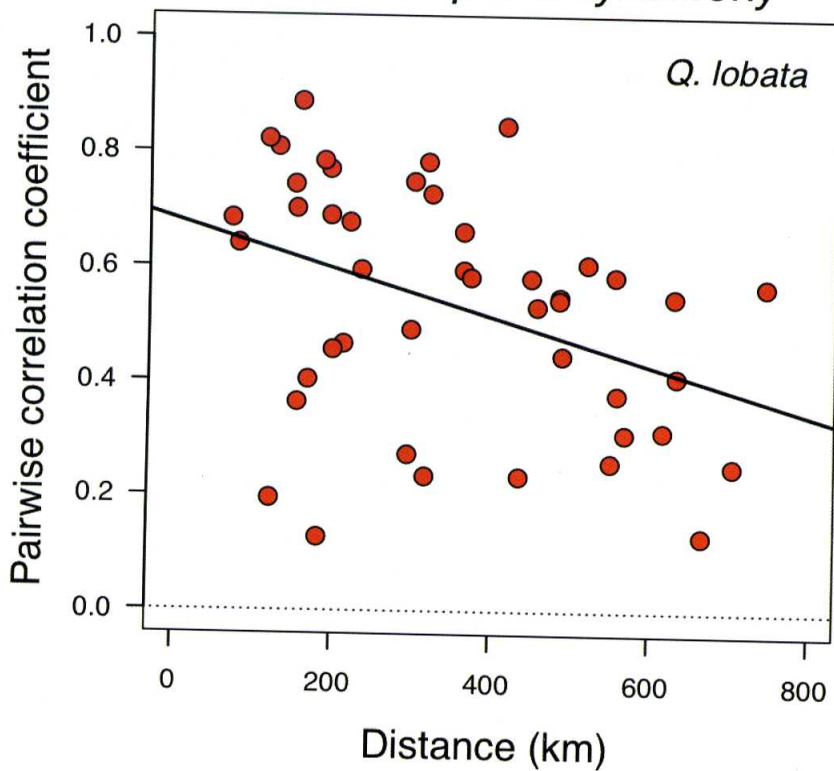


Figure 2/ Spatial synchrony in *Quercus lobata* (valley oak) acorn production. Each point plots, for each pair of sites on the California Acorn Survey, the distance between sites (on the x-axis) versus the correlation between mean acorn production by trees at the two sites (on the y-axis).

synchrony of weather, both temperature and rainfall, is sufficiently high to potentially be driving the observed synchrony in acorn production (Koenig 2002) and is consistent with many aspects of that latter (Koenig and Knops 2013). Models of masting behavior based on resource storage, however, suggest that pollen coupling can similarly produce large-scale spatial synchrony in seed production (Satake and Iwasa 2002a). Little explored is the possibility that genetic similarity among individuals and sites may be a key driver of spatial synchrony, which typically declines with distance in a manner consistent with genetic differentiation.

Recent work by our group on *Q. lobata* (valley oak) suggests that the drivers of spatial synchrony differ considerably depending on the spatial scale of interest. At the relatively small spatial scale of individual trees within a few kilometers of each other, the main factors that appear to drive differences in mean productivity, overall variability, and spatial synchrony are soil nutrients and water availability. At the much larger spatial scale of California, however, where valley oaks were sampled over an area of nearly 2,000 km², the major factor driving mean productivity of the sites and spatial synchrony among sites appears to be weather (the Moran effect). In neither case do genetic differences among individuals or populations appear to play a significant role. Once again, however, additional study and analyses will be required before we gain a complete and satisfying answer to the question of what drives spatial synchrony in the masting behavior of oaks.

Conclusion

Variable and synchronized seed production – masting – is common among oaks, has broad ecological consequences, and has been recognized by humans for centuries. Nonetheless, we are only starting to understand both the evolutionary factors selecting for and the mechanisms driving masting behavior. Oaks – with their relatively large and easily quantified seeds – have and are likely to continue to play a key role in our future, hopefully deeper, understanding of this striking natural phenomenon.

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Photographers. Title page: Walter Koenig (*Quercus lobata* acorns). Photos 1-4: Walter Koenig.

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