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The role of large environmental noise in masting: General model and example from pistachio trees

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ABSTRACT

Masting is synchronous, highly variable reproduction in a plant population, or synchronized boom–bust cycles of reproduction. These pulses of resources have cascading effects through ecosystems, and thus it is important to understand where they come from. How does masting happen and synchronize? In this paper, we suggest a mechanism for this. The mechanism is inspired by data from a pistachio orchard, which suggest that large environmental noise may play a crucial role in inducing masting in plant populations such as pistachio. We test this idea through development and analysis of a mathematical model of plant reproduction. We start with a very simple model, and generalize it based on the current models of plant reproduction and masting. Our results suggest that large environmental noise may indeed be a crucial part of the mechanism of masting in certain types of plant populations, including pistachio. This is a specific example of an important functional consequence of the interactions between stochasticity and nonlinearity.

1. Introduction

Understanding the role of environmental variability in the dynamics of ecological populations has been an area of extensive study. Among the first and most basic results in this area focused on the dynamics of growth for a single population in a varying environment (Lewontin and Cohen, 1969). In this case, the result is that the geometric mean of the growth rate is the best measure of long term growth. This result is not only valid for all levels of environmental noise, but in fact emphasizes the dominant role played by years with very low growth rates. However, even for slightly more complex situations, complete descriptions of growth are difficult to find, and to the extent that simple analytic results are available they have focused primarily on dynamics with small noise (Tuljapurkar, 1990; Lande et al., 2003), with some exceptions for linear systems (Tuljapurkar et al., 2003). Yet, real ecological systems are subject to large environmental influences, and density dependence (nonlinearities) is likely to play a substantial role. The interaction between stochasticity and nonlinearity must obviously be studied within the context of specific systems, and the masting system we study here is one example.

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Masting is the quasi-cyclic and synchronous production of fruits and/or seeds in perennial plants (Kelly, 1994). This variable seed production acts as a resource pulse, causing cascading effects throughout ecosystems, see Ostfeld and Keesing (2000), Vander Wall (2001) for reviews. Thus, it is important to understand the mechanism(s) behind masting behavior. There are generally two competing hypotheses for how masting occurs: resource matching and resource switching (Kelly and Sork, 2002). The resource matching hypothesis contends that interannual variability in seed production is determined by important environmental variables. As such, interannual variability in seed production should mimic the variability seen in key climate variables, most often identified as either precipitation (Piovesan and Adams, 2001) or temperature (Rees et al., 2002). In contrast, resource switching suggests that reproduction is carbon-limited and the individual plant alternates allocation of carbon between reproductive and vegetative structures. Evidence of this behavior is indicated when seed production is significantly more negatively autocorrelated with prior productivity than with any pertinent environmental variables. Resource matching and resource switching are not necessarily mutually exclusive. Both types of behaviors can be exhibited by a single plant population.

The mechanism described in this paper combines the ideas of both resource switching and resource matching: for a given plant, the higher yield was in the previous year, the lower it is in the current year (resource switching), and the steepness of this relationship changes depending upon the environment (resource matching). The addition of resource matching to a model with resource switching adds stochastic variability in the functional relationship between yield in the previous year and yield in the current year, which may be viewed as regional stochasticity, or large environmental noise. The novel idea behind our model is that highly variable regional stochasticity can induce masting, and that it may be crucial to the mechanism of masting in many types of plant populations. This is an example similar to the Moran effect, whereby independent (linear) populations are synchronized by spatially correlated environmental noise over a large spatial scale.

We test the plausibility of this mechanism by developing and analyzing mathematical models of it. We start with a simple mathematical model based on individual-level pistachio tree yield data from a pistachio orchard. This model combines resource switching and regional stochasticity and suggests that masting in pistachio may not occur without the inclusion of this noise. We then study a more general model of masting, based on the adopted model for masting of Satake and Iwasa (Isagi et al., 1997; Satake and Iwasa, 2000, 2002a, b; Iwasa and Satake, 2004; Rees et al., 2002; Crone et al., 2005), combined with the idea of highly variable regional stochasticity. Whereas current models of masting require pollen to be limiting, we show that this model may exhibit masting behavior over a wide range of conditions and in the absence of explicit pollen limitation. In particular, it may explain synchronized masting among different species of plants (Schauber et al., 2002; Ranta et al., 2008; Ranta and Satri, 2007; Koenig and Knops, 1998), as well as masting within species of plants that are either not pollen-limited (Rees et al., 2002; Pías and Guitián, 2006) or are dioecious, as in pistachio.

2. Biological background

The pistachio orchard, or agro-ecosystem, is an excellent experimental model system for the study of masting. Cultivated pistachio trees exhibit masting behavior (Stevenson and Shackel, 1998; Johnson and Weinbaum, 1987), see Figs. 1 and 2. In pistachio, this is also called alternate bearing (Stevenson and Shackel, 1998) because it is thought to occur over a 2-year cycle. The pistachio orchard is resource-rich, highly managed, and all individuals are exposed to a similar climate because of limited topographic change and the small geographic scale of the orchard. Moreover, the trees are genetically similar because they are

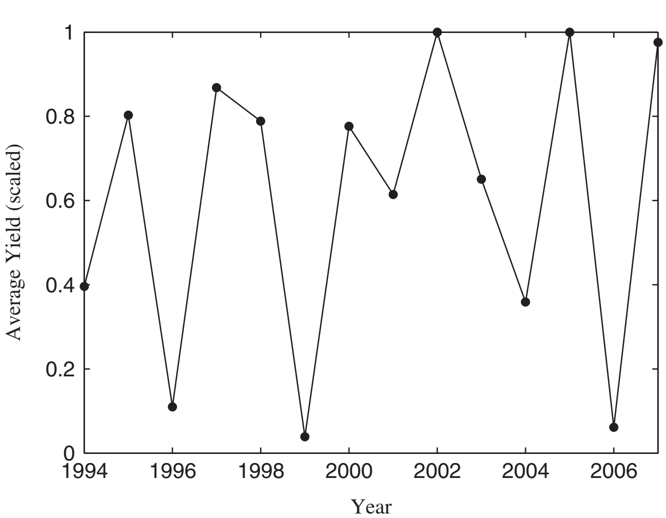

Fig. 1. Historical average pistachio yield (scaled) exhibits quasi-cycic behavior. These data are from about 80 acres. Our data on individual tree yields pertain to the later 6 years of this figure and those individuals for which we have all 6 years of data.

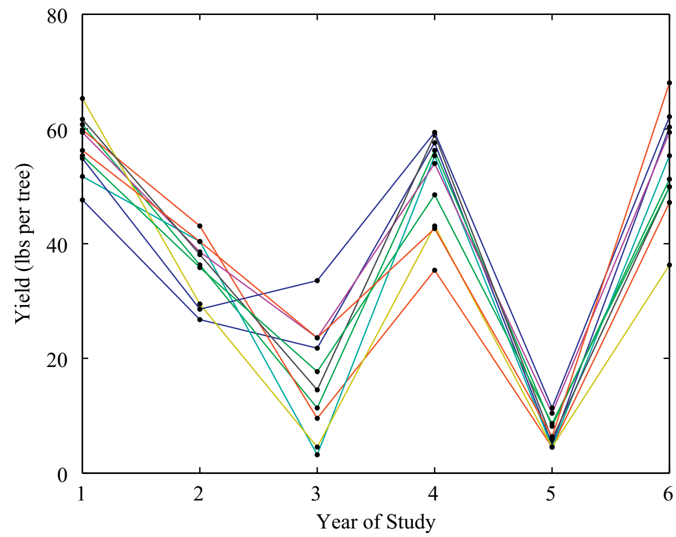

Fig. 2. A sample of the first 10 trees included in the individual tree level data shows synchronized, quasi-cyclic reproduction.

composed of clonal scions and seedling rootstock. Thus, many potential sources of variability present in a natural system are attenuated in the orchard.

The properties of pistachio trees themselves cause them to be an excellent model system for the study of masting as well. Pistachio is an obligate outcrossing wind-pollinated species and is dioecious, male and female flowers occur on separate trees. The male tree is said to pollinate the female tree via the April winds. One can imagine, then, how reproductive success may be sensitive to pertinent weather variables, such as precipitation during the pollination period. The dioecy of pistachio simplifies the dynamics of reproduction relative to monoecious plants (both male and female reproductive organs produced on each individual) because the dynamics of male flowers (pollen source) and female flowers (nut production) are decoupled. This decoupling has two important consequences: one is that the male trees may not have the same resource dynamics as the female trees, and the other is that the amount of pollen available only depends upon the male trees. Thus, observed nut production by female trees may be assumed to only depend upon nut production in the previous year and the amount of pollen available to fertilize the female flowers. This simplifies both data analysis and modeling. Additionally, the fact that pistachio trees produce at least some nuts every year simplifies the modeling process dramatically (Section 3.2).

The relative simplicity of the system, as discussed in the preceding two paragraphs, combined with the extensive amount of individual tree yield data (small spatial scale), gives us the most distinct picture possible for modeling pistachio yield in time. Nonetheless, data on individual tree yields in the pistachio orchard show high levels of noise, both within and between years (Fig. 5). Tree-level data allow us to see two types of noise in the system: variability among trees within a given year (demographic or environmental heterogeneity) and between-year variability in the relationship between current and previous years productivity (regional stochasticity), which occurs at the population level. Next, we describe the individual-level pistachio yield data in detail and examine its properties.

2.1. Individual pistachio tree yield data and its properties

Here, we highlight three important properties of the pistachio yield data: (1) masting behavior near period 2, (2) endogenous resource dynamics, and (3) highly variable regional stochasticity.