



Testing Moran's theorem in an agroecosystem

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The abundance and reproductive effort of populations frequently fluctuate across space and time, a phenomenon known as spatial synchrony. Knowledge of the causes of this behavior underlies the ability to manage species, protect the health of humans and the environment, and increase agricultural sustainability. We used an agroecosystem to test Moran's theorem – spatial synchrony results from environmental entrainment. The controlled conditions of the agroecosystem allowed us to create a highly correlated environment while negating the effects of the alternative hypotheses: dispersal and trophic interactions. Under such conditions, synchrony of fruit production by 4288 trees was high over six years in a 32.5 ha pistachio orchard and occurred at similar temporal frequency as weather patterns demonstrating the Moran effect. The spatial synchrony of fruit production was less than the presumed synchrony of the environment supporting research from microcosms and observational studies showing the Moran effect is degraded by local mechanisms. Indeed even under the homogeneous environment of this system, synchrony declined significantly with distance among trees. We present evidence suggesting that the correlation of the local environment affects intrinsic dynamics to cause these patterns. Our findings demonstrate that the Moran effect is, at minimum, partially responsible for the synchronous fruit production in this system. Agroecosystems are often overlooked in basic ecological research; this experiment provides an example of their comparative advantages for the study of some ecological questions.

Demographic properties of populations (e.g. abundance and reproduction) often fluctuate synchronously across space and time. Such behavior, known as spatial synchrony, has been observed throughout nature and documented in species ranging from plants to parasites and mammals to mollusks (Liebhold et al. 2004a). Despite the prevalence of synchrony, the mechanisms responsible for the phenomenon are unclear. Knowledge of the causes of spatial synchrony is needed to manage species (Harrison and Quinn 1989), protect environmental and human health (Earn et al. 1998, Ostfeld and Keesing 2000), and reduce the effects of agriculture on the environment (Rosenstock et al. 2010).

There are three potential proximate causes of spatial synchrony: (1) correlated environmental conditions, (2) dispersal, and (3) trophic interactions with mobile species. In his seminal work, Moran (1953a, b) postulated that correlated environmental conditions would cause two populations with identical intrinsic dynamics to fluctuate synchronously. This synchronizing effect would later become known as 'the Moran effect' or 'Moran's theorem'. An abundance of observational and theoretical studies support this theory and demonstrate that both spatially and temporally correlated weather patterns synchronize populations (Bjørnstad et al. 1999, Liebhold et al. 2004a). The measured correlation, however, is often less than that of the environment suggesting

that synchrony is affected by local mechanisms (Grenfell et al. 1998, Benton et al. 2001, Peltonen et al. 2002).

Two other factors, dispersal and trophic interactions, have also been shown to synchronize population fluctuations in some cases. Synchrony by dispersal is created through the exchange of individuals or reproductive structures among spatially disjunct oscillators. The ability of dispersal to create synchrony has been demonstrated in theoretical studies (Bjørnstad 2000), microcosms (Fontaine and Gonzalez 2005), and pollen dispersal remains a primary hypothesis for synchronous seed production by perennial plants (Satake and Iwasa 2002a, b). Synchrony may also arise from trophic interactions. The abundance and movement of mobile predator or prey species can synchronize the other. The most compelling examples of these effects come from deciduous forests where population fluctuations of seed production, insects, and their predators are well timed (Satake et al. 2004).

Many theoretical and observational studies examine the contributions of environmental correlation, dispersal, and trophic interactions to spatial synchrony. Bridging modeled and empirical results has proven difficult, however. The challenges of controlling the abiotic and biotic environment in natural landscapes have limited manipulative experiments to microcosms (Benton et al. 2001, Fontaine and Gonzalez 2005). Thus, despite a rich literature, there

has been a paucity of research testing these hypotheses in the field. Here we report the results of field research whose objective was to examine the patterns of spatial synchrony under near perfectly correlated environmental conditions while negating the effects of dispersal and trophic interactions.

Fruit production by perennial plant populations is one of the most extensively studied examples of spatial synchrony (Herrera 1998, Kelly and Sork 2002). The quantity of fruit produced by individuals and populations of trees can vary from no or limited production to an abundant yield among years. Interannual fluctuations are frequently synchronized across large geographic scales, greater than 1000 km for many species (Koenig and Knops 2000). These patterns have been documented in species globally but are especially common in temperate trees species (Kelly and Sork 2002).

The majority of research on synchronous fruit production has focused on population-level measures of reproductive effort over large spatial scales. However, synchrony arises from individuals acting in concert and the ecological mechanisms thought to cause synchrony often take place over smaller scales than usually studied. Therefore, individual trees themselves are a reasonable experimental unit for studies of synchrony. Few studies have measured tree-level synchrony over local scales (Liebhold et al. 2004b, LaMontagne and Boutin 2007). These studies analyzed synchrony over distances between 0 and 10 km and found high degrees of synchrony that decline slightly, if at all, in a few species. The authors note these patterns support the hypothesis that environmental correlation is more likely the ecological cause of synchrony than pollen dispersal and hypothesize that the slight decline in synchrony with distance seen in some species reflects heterogeneous resource availability across the landscape.

The logistical challenge of collecting data on fruit production by individuals impedes the study of synchrony at the tree level. In the most exhaustive studies to date, a few hundred individuals of a single species spread over multiple sites and large distances were observed. Even within highly synchronous populations, among-individual fruit production is variable within years (Koenig et al. 1994, LaMontagne and Boutin 2007), which suggests that studying a limited number of trees may misrepresent the behavior of the population. Furthermore, theoretical evidence suggests the number of individuals observed influences the statistics used to quantify synchrony (Buonaccorsi et al. 2003), but the extent sampling bias affects experimental results is unclear (Koenig et al. 2003).

Manipulative field research that tests the causes of spatial synchrony is needed to bridge the gap between theory and observation. We used an agroecosystem to facilitate addressing this problem. Mechanized harvest equipment and crop management allowed the collection of a greater number of individual-level tree yields under nearly homogenous and resource-rich conditions than has previously been attempted. The objective of this research was to test Moran's theorem by investigating the effect the correlated environment has on synchronous fruit production under conditions of negligible influence of dispersal and in the absence of any significant trophic interactions. Under these conditions, we hypothesized that spatial synchrony of fruit production would be approximately perfectly correlated ($r \approx 1$), uniform across the

orchard, and would occur at similar temporal frequency as relevant weather conditions.

Methods

Species

Pistachio *Pistacia vera* is one of several agricultural species that shows synchronous fruit production (Chung et al. 1995, Stevenson and Shackel 1998). Fruit production alternates between years of high and low production and inter-annual fluctuations may vary by as much as one order of magnitude between consecutive years (Ferguson et al. 1995, NASS 2003). Analysis of the pistachio population studied here shows that fruit production is variable among years, linear, quasi-cyclic, occurs near period two, and within-year coefficients of variation range between 18 and 71% (Lyles et al. 2009, Rosenstock et al. 2010).

Pistachio is a dioecious obligate outcrossing wind-pollinated species. Dioecious species produce male and female flowers on separate individuals. Each male and female tree in our study site consisted of two species grafted together: a seedling rootstock and a clonal scion (the fruiting portion). Female scions were *P. vera* cultivar Kerman, while male scions were *P. vera* cultivar Peters. Both were grafted onto seedling propagated *P. integerrima* rootstock. Neither species has been subject to modern breeding techniques. Thus trees in this system have presumably retained the inherent fruiting patterns of their wild progenitors.

Obligate outcrossing tree species must exchange pollen between individuals for successful fruit production. Data on the distance of pollen dispersal for *P. vera* 'Peters' is lacking. In an experiment on a different pistachio cultivar, Erdogen (1997) found the distance of effective pollen dispersal to be 40 to 80 m.

Study site

The experimental site was a 32.5 ha orchard (416×777 m) located near Lost Hills, Kings County, California ($35^{\circ}86'N$, $119^{\circ}87'W$). The field was located within a single soil type, Panoche Series fine-loam, without any noticeable topographic change across the orchard. The experimental site was planted to a 24:1 female to male ratio in a grid pattern; every fifth tree in every fifth row was a male with 6.4 m between rows and 5.2 m between trees within rows. Females were less than 14 m away from the nearest pollen source. The orchard was reproductively mature, 19 years old, at project commencement and trees were approximately 5 m tall. The orchard was planted in the middle of a larger farm. Besides roads for equipment along the western and eastern edges of the orchard, no geographic features were present that would alter the weather conditions across the orchard.

The grower-controlled production practices were consistent with industry standards (Ferguson et al. 2005). Trees were lightly hand and hedge pruned three times each during the experiment to remove dead branches, control growth, and maintain fruiting sites. Pistachio has no native fruit predators in this region and pesticides were used to control the populations of its primary insect predator, the navel

orangeworm *Amyelois transitella*. On average, only 1.5% of yield showed insect damage (Rosenstock and Brown unpubl.). Nutrients and water were delivered in excess of crop demand through the micro-irrigation system. These systems generally provide these resources with greater than 90% uniformity (Goldhammer 2005).

Data sampling and statistical analysis

Two data-sets were used in this analysis. First, tree-level data on fruit production by 4288 individuals was collected for six years (2002–2007). For this dataset, a precision harvester, The Pistachio Yield Monitor, measured fruit production (Rosa et al. unpubl.). Briefly, the Pistachio Yield Monitor consists of a traditional mechanical pistachio harvester retrofitted with computerized weighing and in-orchard location systems. Tree location data were determined by a redundant mechanical system and crosschecked manually in all rows of the orchard ($n = 66$); all data were examined daily for accuracy. Fruit production was measured as the in-shell wet weight (kg tree^{-1}). The second data-set consisted of population-level (field-level) data on fruit production for the years 1994 to 2007. Field-level data were measured at the processing plant and provided by the grower.

Spatial synchrony of fruit production by pistachio has not previously been measured. We quantified the magnitude and geographic scale of spatial synchrony by applying the nonparametric covariance function (NCF) (Bjørnstad and Falck 2001). The NCF calculates Pearson's correlations between observations at continuous lag distance classes and then connects the mean correlation at each distance with a smoothing spline. Confidence intervals based on 500 resamplings were created to determine significance of this test. Distance classes were limited to less than 280 m to minimize edge effects. Use of Pearson's correlations was reasonable given yields of 4051 of the 4288 trees were normally distributed. The relationship between distance among trees and synchrony was statistically tested with the Mantel statistic with 500 permutations.

Synchrony may be influenced by interannual variability of fruit production and endogenous dynamics. We quantified the degree of interannual fluctuations of fruit production at the individual-level by calculating the coefficients of variation, CV_i . Coefficients of variation were calculated as the ratio of the standard deviation to the mean fruit production for each tree multiplied by 100 for the six-year (2002–2007) time series. Endogenous dynamics were quantified with the autocorrelation function at lag-one, ACF_1 . Calculation of ACF_1 was limited to a single lag because of the strong year-to-year correlation in fruiting pattern characteristic of the species and the short length of the time series. We calculated a spline correlogram of each CV_i and ACF_1 to determine if they showed a spatially random pattern or one similar to the pattern of fruit production. A spline correlogram is a univariate derivative of the NCF and is calculated as described above. The effect of distance on the similarities of CV_i and ACF_1 values were tested with the Mantel statistic with 500 permutations.

Stochastic temporal weather events may cause individuals over the small spatial extent of the orchard (trees were all within 777 m of each other) to fruit synchronously. Similarity

between the frequency of fruiting and climatic variables would suggest an influence of these factors on synchrony. We calculated and compared partial autocorrelation function (PACF) of population-level time series (1994–2007) with climatic variables. PACF calculates the temporal autocorrelation at specified time lags and was used in lieu of the autocorrelation function (ACF) because PACF filters out the effects of correlations at shorter time lags in the calculation of longer lag effects (Shumway and Stoffer 2006). We limited our analysis to lags of up to four years. Because a previous study of means, maxima, and minima of temperature and precipitation was unable to identify a climatic regulator of fruit production in this species (Lobell et al. 2007), we selected three composite weather variables reported to elicit phenological responses and impact fruit production. These were: (1) precipitation during flowering, (2) degree-days during the growing season, and (3) chilling hours. Precipitation during flowering potentially impedes pollen flow. Flowering generally lasts approximately 2.5 weeks and occurs between the third week in March and the first week in May depending on the year (Kallsen et al. 2009). We summed precipitation between 15 March and 6 May to account for all precipitation over this time span. Growing season degree-days, a proxy for the quality of the growing season and net carbon gain, were calculated based on the temperature thresholds of 10 and 38°C between the dates 1 April and 15 September. Last, chilling – a measure of the number of hours of cold temperatures needed to release buds from over-winter dormancy and a factor that can affect flower production and synchrony – was calculated by summing the number of hours below 7.2°C degrees over the winter (between 1 November and 1 March). All weather data were collected at CIMIS weather station no. 21 (Kettleman City), approximately 11 kilometers from the orchard.

Studies of tree-level reproductive output are often limited in their number of observations raising concerns over the potential for sampling bias (Buonaccorsi et al. 2003). In contrast, we assembled an atypically large data-set allowing us to examine the extent of this effect. We compared the NCF values calculated from the full data-set of 4288 trees to values calculated from two subsampled data-sets. The first data-set consisted only of the 4051 trees whose yields were normally distributed, while the second data-set was comprised of 100 randomly chosen trees. To mitigate sampling bias for the second subsampled data-set, we chose 100 trees randomly 500 times, calculated NCF on each, and averaged the NCF across the 500 samples. NCF for both subsampled data-sets were calculated in the same manner as previously described.

All statistical tests were performed using R (R Development Core Team 2006) and the R contributed package 'ncf' (Bjørnstad 2005). Unless otherwise stated, values presented are means \pm SD.

Results

Spatial synchrony

Fruit production was synchronous among individuals. Spatial synchrony of the 4288 trees was highly correlated at

the short distances ($r = 0.87$) and greater than 0.75 across all distance classes examined (Fig. 1). The fitted spline declined over 280 m and did not breach beyond the 95% confidence intervals, which tightly enveloped the spline because of the large number of observations (confidence interval not shown on Fig. 1). Synchrony of fruit production decreased significantly with increasing distance among trees (Mantel test, $p < 0.01$).

Endogenous dynamics and annual fluctuations of fruit production varied among trees and showed distinct nonrandom spatial distributions. Fruit production was negatively autocorrelated over consecutive years (mean $ACF_1 = -0.54 \pm 0.19$). There was an inverse relationship between temporal autocorrelations and distance. The spatial similarity of ACF_1 values extended to 212 m but by 50 m decreased by 78% (Fig. 2). Mean CV_i equaled $56 \pm 12\%$, but ranged between 12% and 95%. The spatial similarity of CV_i gradually declined to 280 m (Fig. 2). Spatial correlations of both ACF_1 and CV_i significantly decreased with distance (Mantel test, $p < 0.01$).

Population-level productivity was more negatively autocorrelated (-0.59) than the weather variables (range -0.37 to 0.25) at a one-year time lag (Fig. 3). At longer lags, between two and four years, the partial autocorrelations of fruit production were within the range of composite weather variables.

Sample size

Results of the NCF calculations were similar regardless of the data-set used. The NCFs calculated from both subsampled data-sets followed a similar declining trend as the NCF calculated from the entire data-set of 4288 trees

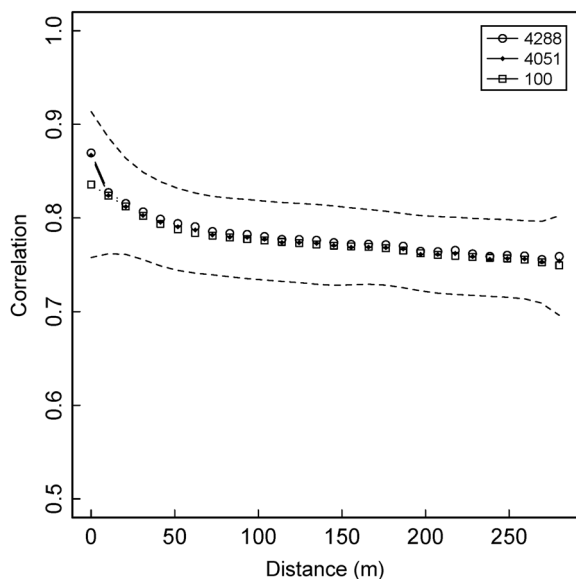


Figure 1. Synchrony of tree-level fruit production over six years calculated by NCF from three data-sets: the full data set of 4288 trees, a data-set composed of the 4051 trees showing normally distributed yields, and the mean NCF of the 500 iterations of 100 randomly sampled trees. Dashed lines represent the 95% confidence envelope of the data-set consisting of the subsamples of 100 randomly sampled trees. Confidence intervals for the data-sets with greater than 4000 observations were narrow and are not shown.

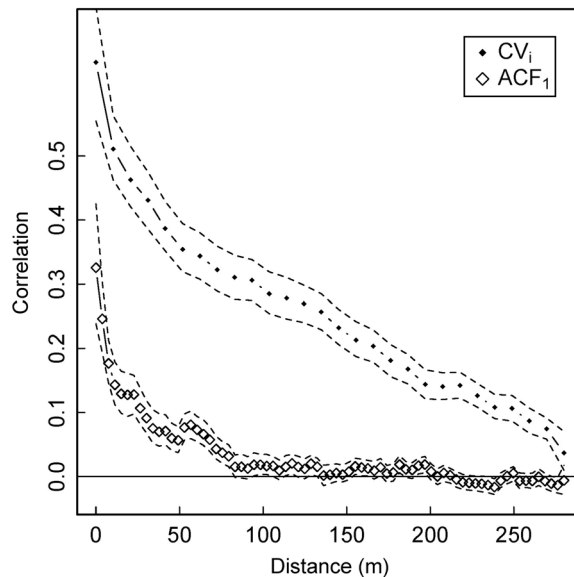


Figure 2. Spatial correlations of serial correlation (ACF_1) and inter-annual variability of tree-level fruit production (CV_i). Dashed lines are 95% confidence intervals from 500 bootstrap resamplings.

(Fig. 1). Mean synchrony based on subsamples of 100 trees was slightly less than the entire dataset at the shortest distances ($r = 0.84$ vs 0.87) but identical at the furthest distance category ($r = 0.75$).

Discussion

Moran's theorem (1953b) suggests that populations (oscillators) with the same intrinsic dynamics will be synchronized by correlated weather conditions. Conditions inherent to this agroecosystem created a unique field setting to test this hypothesis. Based on this theory and experimental setting, we expected synchrony to be high, spatially uniform across

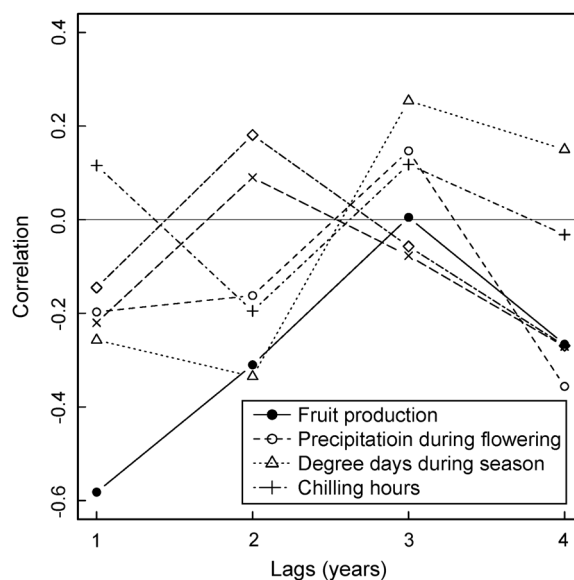


Figure 3. Temporal autocorrelation of population-level productivity and weather variables.

the orchard, and fruit production to take place at a similar temporal frequency of weather patterns.

Our results support Moran's theorem. Under the near uniform conditions of this experiment and negligible influence of pollen dispersal and trophic interactions, synchrony was among the highest documented in the literature. Synchrony was equivalent to or greater than that attributed to correlated environmental conditions in studies of oaks and spruce in natural landscapes over small scales (Liebhold et al. 2004b, LaMontagne and Boutin 2007). It is likely that the greater magnitude of synchrony can be attributed to the homogeneity of conditions and genetics characterizing this system.

Benton et al. (2001) studied the effect of a correlated environment on spatial synchrony under similar conditions – constant resources and without dispersal – using a mite microcosm and found that environmental correlation produced synchronous fluctuations of population abundance. The authors demonstrated that the correlation of spatial synchrony was less than that of the environment thus supporting the observations of Grenfell et al. (1998) in Soay sheep *Ovis aries* in natural landscapes. Synchrony in this orchard showed a pattern consistent with these previous experiments in that the correlation of fruit production was less than the presumed environmental correlation. Dampened spatial synchrony has been suggested to result from the nonlinear dynamics inherent to most ecological systems (Grenfell et al. 1998). Fruit production by pistachio however shows limited evidence of nonlinear dynamics (Lyles et al. 2009), which explains why environmental and spatial synchronies were more similar in magnitude than previous observations.

Although spatial synchrony was high, the expectation of uniform synchrony across the orchard was not met: spatial synchrony declined over the extent of the orchard. Trees nearest each other (less than 10 m) were 19% more synchronous than those furthest apart (280 m), and the effect of distance between trees on synchrony was statistically significant. A fundamental criterion of the Moran theorem is that the distributed oscillators have the same intrinsic dynamics and thus, by extension, if trees in the orchard differed in intrinsic dynamics fruit production may be asynchronous. The 4288 trees in this study clearly exhibited a large variation in their endogenous dynamics, ACF_1 , and temporal fruiting cycles, CV_i . The range of fruiting patterns was unexpected since trees were at the same stage of their life history and Ferguson et al. (2002) suggests that the scion, which was clonal in this orchard, genetically determines interannual variation of fruit production. In addition, the ACF_1 and CV_i showed nonrandom spatial patterns. The spatial distribution of these patterns suggests that some autocorrelated environmental parameter that takes place over small scales influences these processes. Since the trees were genetically similar and the effects of pollen dispersal and trophic interactions were negligible, it seems the patterns and variation of ACF_1 and CV_i and the decline in synchrony result from some unmeasured source of resource heterogeneity.

One plausible explanation for the general declining trend of CV_i are changes in soil physical properties. It is not unusual for soil texture and structure to vary over small spatial scales in agricultural systems. A gradual change in soil would potentially influence nutrient and water holding

capacity and resource availability. Greater resource availability would in turn potentially dampen interannual cycles. Soil samples collected from the top 25 cm of soil in this orchard prior the start of the study show only modest difference in soil physical properties across the orchard (Rosenstock unpubl.). It is currently unknown whether this variation is sufficient to be driving the observed spatial pattern in synchrony, especially given that the effective rooting depth of pistachio trees is 2 m and both nutrients and water were applied in excess of crop demand.

The pattern of ACF_1 values is more difficult to explain by resource heterogeneity. One possible cause is that trees received considerably more or less nutrients or water as a result of heterogeneity of irrigation and fertilization. We suspect this is not the case. In this orchard water and fertilizers are distributed in the irrigation system that generally distributes nutrients and water at greater than 90% efficiency. Irrigation pipes also run in rows and hence should produce discrete linear patterns of resource distribution a pattern that was not reflected in fruit production (Rosa et al. unpubl.). A second potential explanation for the pattern of ACF_1 is pollen dispersal. The scale of decline in ACF_1 correlation was roughly equal to the estimated pollen dispersal distance in a study on a different pistachio cultivar (Erdogen 1997). However, this distance is 2.9 to 3.7 times further than the distance between females and their nearest pollen source and preliminary results of pollen collections in this orchard suggest pollen is equally distributed throughout the orchard (Rosenstock unpubl.). Thus, the factor driving the spatial pattern in serial autocorrelations in our study is currently unknown.

In addition to spatial environmental correlation, the frequency of temporal environmental patterns has also been shown to be important in establishing synchrony (Fontaine and Gonzalez 2005). We found fruit production was within the range of weather correlations at longer time lags suggesting that key weather events take place on the approximate same temporal frequency as fruit production. In contrast to many studies on synchrony, we examined composite weather variables instead of means, maxima, and minima, since prior work examining the relationship between these weather parameters and pistachio production throughout California did not discern a clear link (Lobell et al. 2007). These composite weather variables seem to show greater stochasticity than simple arithmetic measures of weather patterns (Koenig and Knops 2000), a quality important to the extent that species phenology responds more directly to weather signals. Utilizing composite weather variables is analogous to performing a principle components analysis. Therefore our results support the use of this approach when investigating the complex relationships between weather and synchrony (Sork 1993, Lindström et al. 2004).

Because of the mechanized harvest equipment, we were able to collect the most intensively sampled data set of individual-level fruit production and synchrony of trees ever analyzed. This is important because at least one study suggests that sample size may influence the calculation of synchrony (Buonaccorsi et al. 2003). Previous attempts to address this issue have been restricted to theoretical treatments and extrapolations from the fruiting patterns of relatively few individuals per species. The large number of observations in

this study allowed a different but complementary approach. Instead of extrapolating from a limited number of observations, we were able to create subsamples based on collected data. We found that patterns of synchrony calculated from the trees in the three data sets consisting of various numbers of plants (100, 4051 and 4288) were generally similar. That is, we would have potentially reached similar results and conclusions if we had sampled only 100 trees as opposed to 4288. This finding suggests future research on this phenomenon in this system could observe the fruit production of fewer trees than this study. However, extrapolations based on fewer samples would need to be done with caution. The range of synchrony correlations calculated from 500 random subsamples of a 100 trees was greater than the 0.1 or 13% difference between the highest and lowest correlations across most distances. Such a wide range of values indicates that the trees sampled may indeed influence synchrony calculations even in a highly synchronous population.

Conclusion

Bridging theoretical and empirical research on spatial synchrony has proven challenging because of logistical hurdles of experimentation and the complexity of natural landscapes. We capitalized on the replication and control agroecosystems afford to provide a unique opportunity to test Moran's theorem under controlled field conditions. This research demonstrates some comparative advantages of agroecosystems to tackle research questions difficult to address in studies in unmanaged landscapes. Currently, agricultural ecosystems are rarely used for research on spatial synchrony in particular and for basic ecological research in general; more frequent consideration of their utility is warranted.

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