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Variation and synchrony of tree species mast seeding in an old-growth temperate forest

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Abstract

Questions: Mast seeding, synchronous highly variable seed production among years, occurs in many perennial plant species and across diverse plant communities. Two predominant ultimate hypotheses for mast seeding are pollination efficiency and predator satiation, with weather conditions as a proximate cause. Little consensus has been achieved regarding the relative impacts of ultimate selection and proximate weather on variation in seed production. Moreover, mast-seeding studies often focus on a single species or phylogenetically closely related species, while studies on plant communities consisting of tree species with a diversity of reproductive strategies are less common.

Location: The 25-ha Changbaishan temperate forest dynamic plot, Northeast China.

Methods: We used eight-years of seed rain data to characterize the patterns and evaluate underlying selective drivers of mast seeding. We employed generalized linear mixed-effects models to analyze the relationships between interannual variability of mast seeding and weather conditions.

Results: All 20 species in this forest community exhibited high variability in annual seed production, but the magnitude of seed production among species was generally asynchronous across years. Wind-pollinated species had higher interannual variation of seed production than animal-pollinated species, while species dispersed by seed predators and abiotic modes (e.g., wind and gravity) showed little variation. Species responded individually to weather conditions for both temperature and precipitation, and spring phenology at the same year as seed production had a larger effect among species than both the weather conditions of the same summer and season-long lags.

Conclusions: Our findings suggest that pollination efficiency hypothesis hada much stronger effect than predation satiation hypothesis on mast seeding, and weather conditions showed the proximate role of weather drivers in producing the community-wide mast seeding pattern. We emphasize the necessity to simultaneously assess drivers of mast seeding for multiple species within a plant community.

Introduction

Temporal and spatial variations in seed production by plant species drive population dynamics, community assemblages, and biodiversity maintenance in forest ecosystems (Norden et al. 2007; Canham et al. 2014). Mast seeding, the synchronous and highly variable seed production among years by a population of perennial plants (Kelly 2008), is a pattern observed in a large number of species (Janzen 1976; Kelly 1994; Kelly & Sork 2002). Increased pollination efficiency and predator satiation (Janzen 1971) have been considered as two predominant selective factors favoring the evolution of mast seeding (Nilsson & Wästljung 1987), with weather conditions as a proximate explanation(Schauber et al. 2002; Smaill et al. 2011).

The pollination efficiency hypothesis suggests that wind-pollinated plant species (that are beyond the constraint of pollinator satiation) may have greater pollination efficiency during massive and synchronized flowering events (Norton & Kelly 1988; Smith et al. 1990; Koenig et al. 2003). In contrast, mast seeding may decrease the reproductive success of animal-pollinated plant species because animals are more likely to be saturated by large flowering events (Herrera et al. 1998; Kelly et al. 2001). Therefore, it could be expected that wind-pollinated plant species are more likely to display mast seeding than animal-pollinated species. We reviewed 71 studies by searching the literature for interannual variation of seed production in two databases (‘Web of Science’ and ‘Google Scholar’), and found that eleven studies tested the pollination efficiency hypothesis (Appendix S1). Two of these studies explicitly compared the interannual variability in seedfall against the selective factor of pollination vector and found that wind-pollinated species had a larger mean coefficient of variation (CV, a typical measure of variability for mast seeding proposed by Kelly in 1994), than animal-pollinated species, thus supporting the pollination efficiency hypothesis (Herrera et al. 1998; Kelly & Sork 2002). The remaining nine studies focusing on single or several species (Appendix S1) tested the pollination efficiency at the species level, and seven provided support.

The predator satiation hypothesis suggests that large intermittent seed crops can benefit predator-dispersed plants by improving the chance of seeds escaping predation during a mast year (Janzen 1971; Kelly 1994; Fletcher et al. 2010). Predator dispersal (dispersal by animals that predominantly behave as seed predators, Janzen 1971; Herrera et al. 1998) may be affected positively by either directly enhancing dispersal or by improving the chances of some seeds escaping post-dispersal predation (Herrera et al. 1998; Vander Wall 2001). Predator-dispersed species are expected to be temporally much more variable than those dispersed by inanimate means (Herrera et al. 1998). In our literature review, we found 19 studies that tested for this hypothesis, and eighteen of them provided strong evidence (see Appendix S1; Appendix S2b). For instance, a 29-year study on *Pinus ponderosa* showed a markedly lower rate of seed predator attack during mast years compared with years of low seed production (Linhart et al. 2014). Kelly & Sork (2002) conducted a literature-review of 570 mast seeding datasets, and found that predator-dispersed plant species had higher CVs than the species dispersed by other animals, supporting the predator satiation hypothesis.

Weather factors (e.g. temperature and precipitation) have been associated with levels of seed production and can act as a cue or veto for the variation and synchrony in mast seeding (Janzen 1971; Crone et al. 2009). In temperate forests, seasonality in temperature most likely regulates flowering and fruiting phenology (Norton & Kelly 1988; Molau et al. 2005), but the drivers may vary across species. For instance, the proximate weather driver for a very large seed crop (mast year) in *Nothofagus* is a very warm austral summer in the year before flowering (Kelly et al. 2008). However, Pérez-Ramos et al. (2010) showed that interannual patterns of precipitation affected seed production of *Quercus ilex* during the initial (spring) and advanced (summer) stages of acorn maturation. Seed production is complex and can be influenced by a variety of weather factors simultaneously (Schauber et al. 2002; Selås et al. 2002; Krebs et al. 2012). Moreover, weather drivers on mast seeding often showed lag effects (Schauber et al. 2002; Kelly et al. 2008). For instance, a warmer summer and cool winter in the previous year increased seed production for spruce (Selås et al. 2002).

Although both the pollination efficiency and predator satiation hypotheses and the effect of weather conditions on mast seeding have been well-studied and discussed for a diverse array of plant species, several gaps exist in our current understanding of mast seeding. First, little consensus has been achieved regarding the relative importance of ultimate selection and proximate weather on variation in seed production and their concurrent effects (Moreira et al. 2014). We found that most studies (41 of 71; 56%) tested only one driver, whereas only 9 studies (13%) tested multiple drivers (Appendix S2a). Second, community-wide observations of seed production are rare (Appendix S2b; but see Yasaka et al. 2008; Chang-Yang et al. 2015). Among the 71 mast-seeding papers we reviewed, 57 (80.3%) focused on single species or a few phylogenetically closely related species, while only 14 (20%) studied multiple species but in no more than five families (e.g. Howe et al. 2012, Kelly et al. 2013; Appendix S2b). Studies of multiple species within a community are of importance for temperate forests, where many dominant species undergo mast seeding (Silvertown 1980; Kelly & Sork 2002). Simultaneous mast seeding at the same site could benefit many plant species by protecting their seeds from predation and damage, especially for the less common species that might not have large enough numbers on their own to satiate generalist predators (Cadotte et al 2006; Yi et al. 2011). Third, the lack of long-term monitoring of seed production in diverse forest communities hampers our understanding and prediction of plant communities in response to species-specific reproductive pressure and changing climates over time (Ostfeld & Keesing 2000). In our literature review, only eight of 71 studies had more than eight years of seed dispersal data for multiple species across different families (Appendix S2c) and most of these studies focused on species over large geographical areas rather than an entire community. Thus, it is of broad interest to understand how different factors act in driving temporal reproduction patterns of multiple species within a community (Herrera et al. 1998; Kelly & Sork 2002).

In this study, we used an eight-year collection of seed trap data to evaluate the variation and synchrony of seed production for 20 woody plant species in an old-growth temperate forest. We tested the pollination efficiency and predator satiation hypotheses by comparing interannual variation in seedfall (Herrera et al. 1998; Kelly & Sork 2002), and examined how weather conditions influence seeding variability as well. We predicted that: (1) wind-pollinated species had more synchronous and intermittent seed crops over time than animal-pollinated species (Nilsson & Wästljung 1987); (2) predator-dispersed species had a higher interannual variation of seed production than species dispersed by abiotic modes, such as wind and gravity (Janzen 1971); (3) changes in temperature and precipitation were associated with temporal variation of seed production (Smaill et al. 2011).

Materials and methods

Study site

This research was conducted in the 25-ha (500 m × 500 m) Changbaishan temperate forest dynamic plot (42°23′ N, 128°05′ E) in Northeast China, which is located in the broad-leaved Korean pine (*Pinus koraiensis*) mixed forest in the core zone of Changbai Mountain National

Nature Reserve. The climate of the area is characterized by the moist temperate monsoon. Mean annual daily temperature is 2.8°C (–13.7°C in January and 19.6°C in July), and annual precipitation is approximately 700 mm per year, most of which occurs between June and August (Yang & Li 1985).

The Changbaishan plot was established by the Chinese Academy of Sciences (CAS) in collaboration with the Center for Tropical Forest Science - Forest Global Earth Observatory (CTFS-ForestGEO), an international network of more than 63 long-term forest dynamics research sites (Anderson–Teixeira et al. 2015; http://www.forestgeo.si.edu). Within the plot, all free-standing trees at least one centimeter in d.b.h (diameter at breast height) have been mapped, tagged and identified to species (Condit 1998; Hao et al. 2007). During the first census in 2004, a total of 38,902 living stems belonging to 52 species, 32 genera, and 18 families were recorded. The dominant tree species included *Pinus koraiensis* (PIKO), *Tilia amurensis* (TIAM), *Quercus mongolica* (QUMO), *Fraxinus mandshurica* (FRMA), *Ulmus japonica* (ULJA) and *Acer mono* (ACMO) (Hao et al. 2007).

Seed rain data

In 2006, 150 seed traps were set up in a relatively regular pattern within the 25-ha plot. The maximum distance among seed traps was 31 m (Li et al. 2012). Each trap was 0.5 m^2 (0.71 m × 0.71 m) in area and was made of fine, flexible mesh supported on a PVC structure. Seeds were collected biweekly from May to December and once per month from January to April. All seeds, fruits, seed-bearing fruit fragments, flowers, capsules and other reproductive structures that fell into seed traps were identified and counted (Zhang et al. 2008; Li et al.

2012). Seeds were judged to be mature if they were plump, and otherwise considered as immature. For species with more than one seed per fruit, seed number within each fruit was counted as the mean seed count per mature fruit for each species (Li et al. 2012).

Seed production was determined by the number of mature seeds of each species falling into all 150 traps. All seed rain data during eight full phenological years from May 2006 to April 2014 were used for this study. To ensure data reliability for the interannual variation of seed production for the community level, we excluded the species with fewer than 30 seeds across eight years (most of them came from only one or two seed traps), and a total of 20 species were included to test the pollination efficiency and predator satiation hypotheses.

Reproductive traits

We assigned reproductive strategies (pollination and dispersal vectors) to each of the 20 species. Pollination vectors were classified into animal-pollinated (insect), wind-pollinated, or both (Liu 1955; Li et al. 2012; Wang et al. 2014). Ten species were animal-pollinated, six were wind-pollinated, and four could be pollinated by both wind and animals (Table 1). Dispersal modes included animal-dispersed, gravity-dispersed, or wind-dispersed, and four species were animal-dispersed, three gravity-dispersed and thirteen wind-dispersed, and all four animal-dispersed species were predator-dispersed (Table 1).

Weather data

Daily temperature and precipitation data were obtained for the years 2005-2014 from the Meteorological Observation Field of Changbai Mountain Forest Ecosystem Station, Chinese Academy of Sciences (~1.5 km distance from our plot). Precipitation was recorded once per day, and temperature was recorded three times per day, at 8:00, 14:00 and 20:00. To test the effects of weather cues on mast seeding, we used these daily data to calculate seasonal averages (summer (June-August) and winter (December-February) of the previous year, spring (March-May) and summer of the current year), including mean maximums, mean minimums, mean values of temperature and total precipitation, as well as these variables during flowering and fruiting periods of the current year. According to Li et al. (2012) and our field observations (2013–2015), the flowering periods for the seven mast-seeding species were from May to July (Table 2) and the fruit ripening period were mainly from July to September.

Statistical analyses

Variability and synchrony in seed production

For each species, to evaluate the strength of interannual variation of seed production during the eight-year period we used the coefficient of variation (CV_{year}), the standard deviation of annual seed abundance divided by the mean (Kelly 1994). To divide years into mast years and non-mast years, we used the standardized deviate method (see LaMontagne & Boutin2009). In assessing mast-seeding patterns, we only included species that occurred in more than five seed traps (we did not count two traps as sampling separate trees if they were spatially adjacent) where each trap had at least 100 seeds each of the species caught during eight-year period. As a result, four species were included in these analyses of mast seeding (Table 1).

To detect the temporal synchrony patterns on seed production among species, Spearman correlations were used for all pairwise comparisons of species based on raw seed counts. Spearman correlations were used because the data were not bivariate normally distributed (Quinn & Keough 2002; LaMontagne & Boutin 2007). We were particularly interested in the temporal synchrony of congeneric species (one pair of *Tilia*, one pair of *Populus*, and 21 pairs for seven *Acer* species). This is because congeneric species tended to share biological similarities and annual variability in seed output depended significantly on taxonomic affiliation at the genus and species levels (Herrera et al. 1998).

Testing for pollination efficiency and predator satiation hypotheses

Although dataset on fruit set in large flowering events and seed predation in masting years are much beneficial to evaluate pollination efficiency and predator satiation, the strong associations between annual variability in seed production and pollination vectors or dispersal modes have been widely accepted (Kelly 1994; Herrera et al. 1998). Thus to test for differences in CV_{year} among the 20 species with different reproductive strategies we conducted a weighted analysis of variance (ANOVA), taking into account that differences in seed abundance among species may affect the reliability of CV_{year}. CV_{year} values were weighted by the total seed number per species (Queenborough et al. 2009). Prior to ANOVA analysis, Shapiro-Wilk and Bartlett tests were used to evaluate the assumptions of normality and equal variance (Zar 1999) for all three levels of pollination vector (*P* = 0.09, 0.40) and dispersal mode(*P* = 0.08, 0.85), with each test shown respectively.

Weather drivers on seed production

Weather conditions influence reproductive dynamics through either cueing (usually favorable, e.g. warm summers, Kelly & Sork 2002; Schauber et al. 2002) or vetoing (usually unfavorable, e.g. frosts or rain, Kelly *et al*. 2008). We chose a subset of species as examples to examine responses to weather factors, through taking advantage of specific-species plant biology. We selected PIKO, the key coniferous species in the mixed forest, and species with more than 5,000 seeds across the eight years (Table 1 & 2). For these seven species, we used a generalized linear mixed–effects model (GLMM) to model their seed production from 2006 to 2014 as a function of weather conditions (Blume et al. 2007). The GLMM model included a Poisson–distributed response variable of the total seed abundance of all species falling into each seed trap across years, with the weather conditions as independent variables, and the individual trap code and the year included as random effects. We standardized the values of the continuous explanatory variables by subtracting the mean value of the variable and dividing by one standard deviation (Schielzeth 2010). To reduce multicollinearity, we ran pairwise correlations among all climate variables, and reduced our set of variables using a correlation threshold of 0.7 (Dormann et al. 2013) resulting in retaining two to six weather variables for each species.

All statistics were calculated in R 3.2.2 (R Core Team 2015). GLMM was carried out in the R package ‘lme4’ (Bates et al. 2010).

Results

Variability and synchrony in seed production

For the 20 plant species studied, a total of 480,528 mature seeds were collected during the eight years (Table 1). Seed production showed substantial temporal variation (Figs 1 & 2). The coefficient of variation (CV_{year}) of seed production ranged from 0.56, indicating low variability across years, to 2.78, with the median of 1.43. Seventeen of the twenty species had a CV > 1 (two others were 0.990 and 0.991). All four species used to do masting analyses were undergoing mast seeding during 2006-2014. Among these four species, ACPS and PIKO had one mast year during the period of the study, while FRMA and ULJA had two mast years (Fig. 2).

The two *Tilia* species (TIAM and *T. mandshurica*) were statistically synchronous over time (r_s= 0.86, P< 0.001), while the two *Populus* species were not significantly synchronous over time (r_s = 0.57, P = 0.15). For the seven *Acer* species, only five out of 21 pairs showed significant synchrony (Appendix S3). In addition, we found significant synchrony between PIKO and *Corylus mandshurica* (r_s= 0.91, P< 0.001), and between PIKO and QUMO (r_s= 0.76, P = 0.03); these three species are all animal-dispersed (Appendix S3, Table 1).

Testing for pollination efficiency hypotheses and predator satiation

For the pollination efficiency hypothesis, wind-pollinated species had a significantly higher mean CV_{year} than either animal-pollinated species or the species pollinated by both wind and animals (F = 4.66, P = 0.024, Fig. 3a). With respect to the predator satiation hypothesis, the weighted ANOVA showed that the mean CV_{year} was marginally significantly different among dispersal modes (Fig. 3b), with predator-dispersed species tending to have a lower CV_{year} than species with other dispersal vectors (F = 3.54, *P* = 0.052, Fig. 3b).

Weather drivers on seed production

Weather factors during spring flowering and seed ripening had significant effects on seed production for six of the seven focal species (except for TIAM; Table 2). During spring, both low temperature and high precipitation reduced seed production for ULJA, ACMO, ACPS and QUMO. Species varied their responses to similar weather conditions. For example, precipitation during flowering had different effects on seed production for FRMA (positive) and PIKO (negative), and precipitation during summer showed positive effect for FRMA and negative for QUMO (Table 2). Lag effects were also significant for some species, for example, seed production of ACPS was significantly positively associated with minimum temperature of previous summer and mean maximum temperature of the previous winter. Overall, the current spring phenology had a stronger effect on seed production than both the weather conditions of the current summer and season-long lags.

Discussion

Using eight-years of seed trap data from a 25-ha old-growth temperate forest community, we examined the variation and synchrony of seed production of multiple species, and tested the validity of pollination efficiency, predator satiation and weather drivers on explaining interannual variation in seed production. Our results support the hypothesis that pollination efficiency can select for the evolution of mast seeding (Nilsson & Wästljung 1987), but provide only weak support for the predation satiation hypothesis (Janzen 1971; Kelly 1994). The fact that correlations between seed production of six out of seven species used to examine responses to weather factors and weather conditions were significant indicates the proximate role of weather drivers in producing the mast seeding pattern.

Our findings contribute to the growing literature supporting the pollination efficiency hypothesis (Nilsson & Wästljung 1987; Norton & Kelly 1988; Kon et al. 2005; Moreira et al. 2014). In general, animals (e.g. insects) are more likely to provide diseconomies of scale since stronger competition for pollinators in animal-pollinated plant species could actually decrease pollination success when high flowering effort occurs (Rathcke & Lacey 1985; Herrera et al. 1998; Kelly et al. 2001). We found that wind-pollinated plant species had higher interannual variation in seed production than animal-pollinated plants, suggesting that pollination efficiency is a selective factor favoring the evolution of mast seeding (Kelly & Sork 2002). Although previous studies showed that community-wide synchrony of large flowering events among plants could augment the visitation rates by attracting more pollinators (Augspurger 1981), for animal-pollinated species, the reproductive disadvantages that only a limited proportion of flowers can be visited and pollinated during mast years was supported (Herrera et al. 1998).

Regarding the predation satiation hypothesis, we found that interannual variation in seed production was only slightly stronger among predator-dispersed taxa than abiotically dispersed taxa. Further, among the four predator-dispersed species, only two pairs (PIKO and

QUMO; PIKO and COMA) showed significant interspecific synchrony. These results provide only a limited contribution to the ‘predation satiation’ hypothesis. Several factors may have contributed tothese results. First, spatial and temporal variation in seed production can lead to fluctuations in seed-hoarding rates and prey switching, which might facilitate seed escape from animal predation at low levels of seed production (Fletcher et al. 2010). Having seed escape from predators is undoubtedly one of the major ecological and evolutionary determinants of mast seeding in polycarpic plants (Ims 1990; Herrera et al. 1998). Second, seed availability during relatively low-seed years may still satiate the hoarding activity of predators (e.g. *Cydia fagiglandana* in Nilsson & Wästljung 1987; *Picea glauca* in Fletcher et al. 2010). In our study, among the four predator-dispersed species, PIKO, QUMO and COMA, had seed production proportional to their population sizes. In addition, asynchrony among the four predator-dispersed species may reflect inconsistencies among plant species in the benefits and costs of synchronous seed production between-species (e.g., facilitation and competition) (Herrera et al. 1998; Razafindratsima & Dunham 2016).

Weather conditions can influence reproductive dynamics through either resource budgets (e.g., weather affecting resources; Satake & Bjørnstad 2008) or synchronizing plants by cueing or vetoing (Kelly & Sork 2002; Kelly et al. 2008). On one hand, interannual fluctuations in seed production are consistent with the idea that weather affects resources and regulates interannual seed production (Koenig et al. 1994; Kon et al. 2005; Satake & Bjørnstad 2008). That is, resources accumulated during a period of low seed production might be sufficient for more than one year of heavy seed production (Żywiec et al. 2012). On the other hand, we found strong correlations between seed production and weather conditions, which is consistent with previous studies that show that weather triggers the variation and synchrony in mast seeding (McKone, Kelly & Lee, 1998; Schauber *et al*. 2002; Smail *et al*. 2011). Species varied greatly in their response to weather conditions for both temperature and precipitation over time. However, community-wide ecological processes probably are not influenced by a single weather factor, but rather a suite of weather variables accompanied by the interactions between a suite of life-history strategies. For instance, weather-driven environmental filtering may cause seasonal fluctuations in the phylogenetic patterns of phenology (e.g. flowering and seed production) in a community (Razafindratsima & Dunham 2016).We found higher sensitivity of seed production to spring flowering for six of seven focal species than the current summer and season-long lags (only for individual species). This suggests that the pattern of spring phenology plays an important role in the seed production pattern of this temperate forest community. Changes in spring phenology of flowering (Fitter & Fitter 2002; Parmesan 2007) associated with climate warming are common in temperate forests. These analyses can improve our ability to predict community-wide reproductive regeneration and dynamics (Ostfeld & Keesing 2000) under climate warming.

Due to the restricted length of seed rain collection (eight years) in our study, we cannot detect critically the periodicity in interannual seed production. For example, oak species have been found to undergo mast seeding in several temperate forests (e.g. Espelta et al. 2008; Pearse et al. 2014), but our eight years of data for oak species in the Changbaishan plot showed relatively small variation in interannual seed production. The ongoing efforts to continually monitor long-term dynamics of seed dispersal in the CTFS-ForestGEO network, including our study plot, will greatly benefit our understanding of mast seeding, especially of multiple species at a plant community, in the near future (Anderson–Teixeira et al. 2015). Mass flowering and mast seeding has been shown to be a community-wide phenomenon at the Lambir CTFS-ForestGEO site in Malaysiaand the 25-ha Fushan forest plot of northern Taiwan (Sakai et al. 1997; Chang-Yang et al. 2015). In addition, further field work on measuring more related parameters of flower production and seed predation rate could benefit our conclusions and understanding of mast seeding ecology.

In conclusion, our results suggest that within a temperate forest community that the spatial and temporal seed production patterns of species is an adaptive reproductive strategy based on the species' pollination vector (abiotic or biotic) overlaid on the influence of weather (Kelly & Sork 2002). This finding highlights the necessity to simultaneously consider both evolutionarily selective mechanisms and proximate weather causes on both population and community levels. Further studies of reproductive synchrony (e.g., flowering and seed production) in plants deserve special consideration in their own right (Ims 1990). The improved knowledge of interannual variation and causes of seed production, especially mast seeding, on an individual and community level will increase our understanding of plant's life-history evolution (Curran & Leighton 2000), vegetation dynamics (Ostfeld & Keesing 2000) and plant-animal interactions (Herrera et al. 1998; Curran & Leighton 2000; Hegland et al. 2009) under a changing climate.

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References

Augspurger C.K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators in *Hybanthus prunifolius* (Violaceae). *Ecology*, 62: 775–788.

Bates, D., Maechler, M. & Bolker, B. 2011 lme4: Linear mixed–effects models using S4 classes. http://cran.R–project.org/package=lme4. R package version 0.999375–42.

Blume, J.D., Su, L., Olveda, R.M. & McGarvey, S. T. 2007. Statistical evidence for GLM regression parameters: a robust likelihood approach. *Statistics in Medicine*, 26:2919–2936.

Cadotte, M.W., Mcmahon, S.M. & Fukami, T. 2006. *Conceptual Ecology and Invasion Biology*. Springer, Berlin.

Canham, C.D., Ruscoe, W.A., Wright, E.F. & Wilson, D.J. 2014. Spatial and temporal variation in tree seed production and dispersal in a New Zealand temperate rainforest. *Ecosphere*, 5: art49.

Chang-Yang, C.H., Sun, I.F., Tsai, C.H., Lu, C.L. & Hsieh, C.F. 2015. ENSO and frost co–determine decade–long temporal variation in flower and seed production in a subtropical rainforest. *Journal of Ecology*, doi: 10.1111/1365–2745.12481.

Cheng, B.R., Xu, G.S., Ding, G.F., Zhang, Y.H. & Wang, W. 1984. Litterfall and its nutrient content of dominant types of forest ecosystem in Changbai Mountain. *Chinese Forest Ecosystem Research*, 4: 19–24.

Crone, E.E., Miller, E. & Sala, A. 2009. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast–seeding in a perennial wildflower. *Ecology Letters*, 12: 1119–1126.

Curran, L.M. & Leighton, M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast–fruiting Dipterocarpaceae. *Ecological Monographs*, 70: 101–128.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., GarcíaMarquéz, J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Munkemuller, T., McClean, C., Osborne, P.E., Reineking, B., Schroder, B., Skidmore, A.K., Zurell, D. & Münkemüller, T. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36: 27–46.

Espelta, J.M., Cortés, P., Molowny–Horas, R., Sánchez–Humanes, B. & Retana, J. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. *Ecology*, 89: 805–817.

Fitter, A.H. & Fitter, R.S.R. 2002. Rapid changes in flowering time in British plants. *Science*, 296: 1689–1691.

Fletcher, Q.E., Boutin, S., Lane, J.E., LaMontagne, J.M., McAdam, A.G., Krebs, C.J. & Humphries, M.M. 2010. The functional response of a hoarding seed predator to mast seeding. *Ecology*, 91: 2673–2683.

Hao, Z.Q., Zhang, J., Song, B., Ye, J. & Li, B.H. 2007. Vertical structure and spatial associations of dominant tree species in an old–growth temperate forest. *Forest Ecology and Management*, 252: 1–11.

Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.L. & Totland, Ø. 2009. How does climate warming affect plant–pollinator interactions? *Ecology Letters*, 12: 184–195.

Herrera, C.M., Jordano, P., Guitián, J. & Traveset, A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *The American Naturalist*, 152: 576–594.

Ims, R.A. 1990. On the adaptive value of reproductive synchrony as a predator–swamping strategy. *American Naturalist*, 136: 485–498.

Janzen, D.H. 1971. Seed predation by animals. *Annual review of ecology and systematics*, 2: 465–492.

Janzen, D.H. 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics*, 7: 347–391.

Kelly, D. & Sork, V.L. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics*, 33: 427–447.

Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution*, 9: 465–470.

Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S. & Westfall, R.D. 2003. Dissecting components of population–level variation in seed production and the evolution of masting behavior. *Oikos*, 102: 581–591.

Koenig, W.D., Knops, J.M., Carmen, W.J., Stanback, M.T. & Mumme, R.L. 1994. Estimating acorn crops using visual surveys. *Canadian Journal of Forest Research*, 24: 2105–2112.

Koenig, W.D., Mumme, R.L., Carmen, W.J. & Stanback, M.T. 1994. Acorn production by oaks in central coastal California: variation within and among years. *Ecology*, 75: 99–109.

Kon, H., Noda, T., Terazawa, K., Koyama, H. & Yasaka, M. 2005. Proximate factors causing mast seeding in *Faguscrenata*: the effects of resource level and weather cues. *Canadian Journal of Botany*, 83: 1402–1409.

Krebs, C.J., LaMontagne, J.M., Kenney, A.J. & Boutin, S. 2012. Climatic determinants of white spruce cone crops in the boreal forest of southwestern Yukon. *Botany–Botanique*, 90: 113–119.

LaMontagne, J.M. &Boutin, S. 2007. Local–scale synchrony and variation in mast seed production patterns of *Piceaglauca*. *Journal of Ecology*, 95: 991–1000.

Li, B.H, Hao, Z., Bin, Y., Zhang, J. & Wang, M. 2012. Seed rain dynamics reveals strong dispersal limitation, different reproductive strategies and responses to climate in a temperate forest in northeast China. *Journal of*

Vegetation Science, 23: 271–279.

Liu, S. 1955. *Woody plant photography records in Northeast China*. Science Press, Beijing, China.

McKone, M.J., Kelly, D. & Lee, W.G. 1998. Effect of climate change on mast–seeding species: frequency of mass flowering and escape from specialist animal seed predators. *Global Change Biology*, 4: 591–596.

Molau, U., Nordenhäll, U. & Eriksen, B. 2005. Onset of flowering and climate variability in an alpine landscape: a 10–year study from Swedish Lapland. *American Journal of Botany*, 92: 422–431.

Moreira, X., Abdala-Roberts, L., Linhart, Y.B. & Mooney, K. A. 2014. Masting promotes individual–and population–level reproduction by increasing pollination efficiency. *Ecology*, 95: 801–807.

Nilsson, S.G. & Wästljung, U. 1987. Seed predation and cross–pollination in mast–seeding beech (*Fagussylvatica*) patches. *Ecology*, 68: 260–265.

Norden, N., Chave, J., Caubère, A., Châtelet, P., Ferroni, N., Forget, P.M. &Thébaud, C. 2007. Is temporal variation of seedling communities determined by environment or by seed arrival? A test in a neotropical forest. *Journal of Ecology*, 95: 507–516.

Norton, D.A. & Kelly, D. 1988. Mast seeding over 33 years by *Dacrydium cupressinum Lamb. (rimu)* (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology*, 2: 399–408.

Ostfeld, R.S. & Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution*, 15: 232–237.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421: 37–42.

Pearse, I.S., Koenig, W.D. & Knops, J.M.H. 2014. Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos*, 123: 179–184.

Pérez-Ramos, I.M., Ourcival, J.M., Limousin, J.M. & Rambal, S. 2010. Mast seeding under increasing drought: results from a long–term data set and from a rainfall exclusion experiment. *Ecology*, 91: 3057–3068.

Queenborough, S.A., Mazer, S.J., Vamosi, S.M., Garwood, N.C., Valencia, R. & Freckleton, R.P. 2009. Seed mass, abundance and breeding system among tropical forest species: do dioecious species exhibit compensatory reproduction or abundances? *Journal of Ecology*, 97: 555–566.

Quinn, G.P. & Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.

R Core Team. 2015. R: A language and environment for statistical computing. Version 3.2.2.

Rathcke, B. &Lacey, E.P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, 16: 179–214.

Razafindratsima, O.H. & Dunham. A.E. 2016. Co-fruiting plant species share similar fruit and seed traits while phylogenetic patterns vary through time. *Journal of Ecology*, doi: 10.1111/1365-2745.12645.

Schauber, E.M., Kelly, D., Turchin, P., Simon, C., Lee, W.G., Allen, R.B. & Brockie, R.E. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology*, 83: 1214–1225.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in*

Ecology and Evolution, 1: 103–113.

Selås, V., Piovesan, G., Adams, J.M. & Bernabei, M. 2002. Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research*, 32: 217–225.

Silvertown, J.W. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society*, 14: 235–250.

Smaill, S.J., Clinton, P.W., Allen, R.B. & Davis, M.R. 2011. Climate cues and resources interact to determine seed production by a masting species. *Journal of Ecology*, 99: 870–877.

Smith, C.C., Hamrick, J.L. & Kramer, C.L. 1990. The advantage of mast years for wind pollination. *American Naturalist*, 136: 154–166.

Vander Wall, S.B. 2002. Masting in animal–dispersed pines facilitates seed dispersal. *Ecology*, 83: 3508–3516.

Wang, Y.Y., Shi, S., Lin, F., Yuan Z.Q., Ye, J., Wang, X.G. & Hao, Z.Q. 2014. Reproductive traits and their correlation among woody plants in a broadleaf–Korean pine (*Pinus koraiensis*) mixed forest in Northeast China. *Chinese Science Bulletin* (Chinese Version), 59: 2407–2415.

Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P. & Foster, R.B. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology*, 21: 307–315.

Yang, H. & Li, D. 1985. Distribution patterns of dominant tree species on northern slope of Changbai Mountain. *Chinese Forest Ecosystem Research*, 5: 1–14.

Yasaka, M., Takiya, M., Watanabe, I., Oono, Y. & Mizui, N. 2008. Variation in seed production among years and among individuals in 11 broadleaf tree species in northern Japan. *Journal of Forest Research*, 13: 83–88.

Yi, X.F., Yang, Y.Q. & Zhang, Z.B. 2011. Intra–and inter–specific effects of mast seeding on seed fates of two sympatric *Corylus* species. *Plant Ecology*, 212: 785–793.

Zar, J.H. 1999. *Biostatistical Analysis*. 4th ed. Prentice–Hall, Upper Saddle River, New Jersey, USA.

Zhang, J., Hao, Z.Q., Li, B.H., Y, J., Wang, X.G. & Yao, X.L. 2008. Composition and seasonal dynamics of seed rain in broad–leaved Korean pine (*Pinus koraiensis*) mixed forest, Changbai Mountain. *ActaEcologicaSinica*, 28: 2445–2454.

Żywiec, M., Holeksa, J. & Ledwoń, M. 2012. Population and individual level of masting in a fleshy–fruited tree. *Plant Ecology*, 213: 993–1002.

Supporting information

Appendix S1 The list of 71 papers included in the literature-review in Figure 1.

Appendix S2 Summary of a literature review of 71mast seeding studies in forest ecosystems.

Appendix S3. Interspecific synchrony based on Spearman correlations among all pairwise comparisons of species with n = 8 (year).

Table legends

Table 1 Taxonomic information and masting measures of species seeds collected ordered by the descending seed abundance in a 25-ha temperate forest plot. CV_{year} represents the interannual variation of seed number for each species. Note: '*' indicates that these species were used to identify the mast-seeding behaviour.

Species name	**Species code**	**Family**	**Total seed abundance**	**Mean CV_{year}**	**Dispersal mode**	**Pollination vector**
Tiliaamurensis	TIAM	Tiliaceae	282,115	0.991	Gravity	Insect
Fraxinusmandshurica	FRMA*	Oleaceae	108,065	1.093	Wind	Insect
Ulmus japonica	ULJA*	Ulmaceae	35,277	1.345	Wind	Wind
Acer mono	ACMO	Aceraceae	19,517	0.990	Wind	Wind & Insect
Acer pseudo–sieboldianum	ACPS *	Aceraceae	15,250	1.421	Wind	Wind & Insect
Quercusmongolica	QUMO	Fagaceae	7,792	0.560	Animal	Insect
Betulaplatyphylla	BEPL	Betulaceae	3,100	2.781	Wind	Wind
Acer barbinerve	ACBA	Aceraceae	3,094	1.849	Wind	Insect
Pinuskoraiensis	PIKO *	Pinaceae	2,327	1.970	Animal	Wind
Acer tegmentosum	ACTE	Aceraceae	1,431	1.670	Wind	Wind & Insect
Tiliamandshurica	TIMA	Tiliaceae	579	1.345	Gravity	Insect
Acer mandshuricum	ACMA	Aceraceae	502	1.098	Wind	Insect
Populuskoreana	POKO	Salicaceae	414	1.116	Wind	Wind
Maackiaamurensis	MAAM	Leguminosae	311	2.296	Gravity	Insect
Acer triflorum	ACTR	Aceraceae	261	1.330	Wind	Wind & Insect
Populusussuriensis	POUS	Salicaceae	164	1.123	Wind	Wind
Corylusmandshurica	COMA	Betulaceae	122	1.593	Animal	Wind
Malusbaccata	MABA	Rosaceae	110	1.814	Animal	Insect
Syringareticulata	SYRE	Oleaceae	58	1.869	Wind	Insect
Acer ginnala	ACGI	Aceraceae	39	1.104	Wind	Insect

Table 2 Response of seed production to weather variables over time. The significance of each weather factor was quantified using generalized linear mixed model (GLMM) and the individual trap code and collected year were used as random factors. T represents temperature and P represents precipitation. The full names of these species can be found in Table 1. Note: significance values from the GLMM are tested using z-score statistic and indicated by asterisks (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

Weather variables	TIAM	FRMA	ULJA	ACMO	ACPS	QUMO	PIKO
Flowering time	June~July	June	May	May	May	May	June
MaxT_ May			0.535(*P* = 0.077)		–0.034 *		
P_ June		0.951***					–0.446 **
MaxT_Spring					0.96***	0.240**	
MinT_Spring				–0.481*		–0.244**	
P_ Spring			–0.979 *	–0.644*	–0.844***		
MaxT_Summer		1.454***					
MinT_Summer		–0.564**					
P_Summer		1.253***			0.116***	–0.395***	
MinT_PreSummer					0.151***		
MaxT_PreSummer					–1.314***		
MaxT_PreWinter					0.564***		

Figure 1 Interannual seed production for 16 species (removing the four species presented in Fig. 2) in the order of descending seed abundance between the years 2006 and 2014. The full names of these species can be found in Table 1.

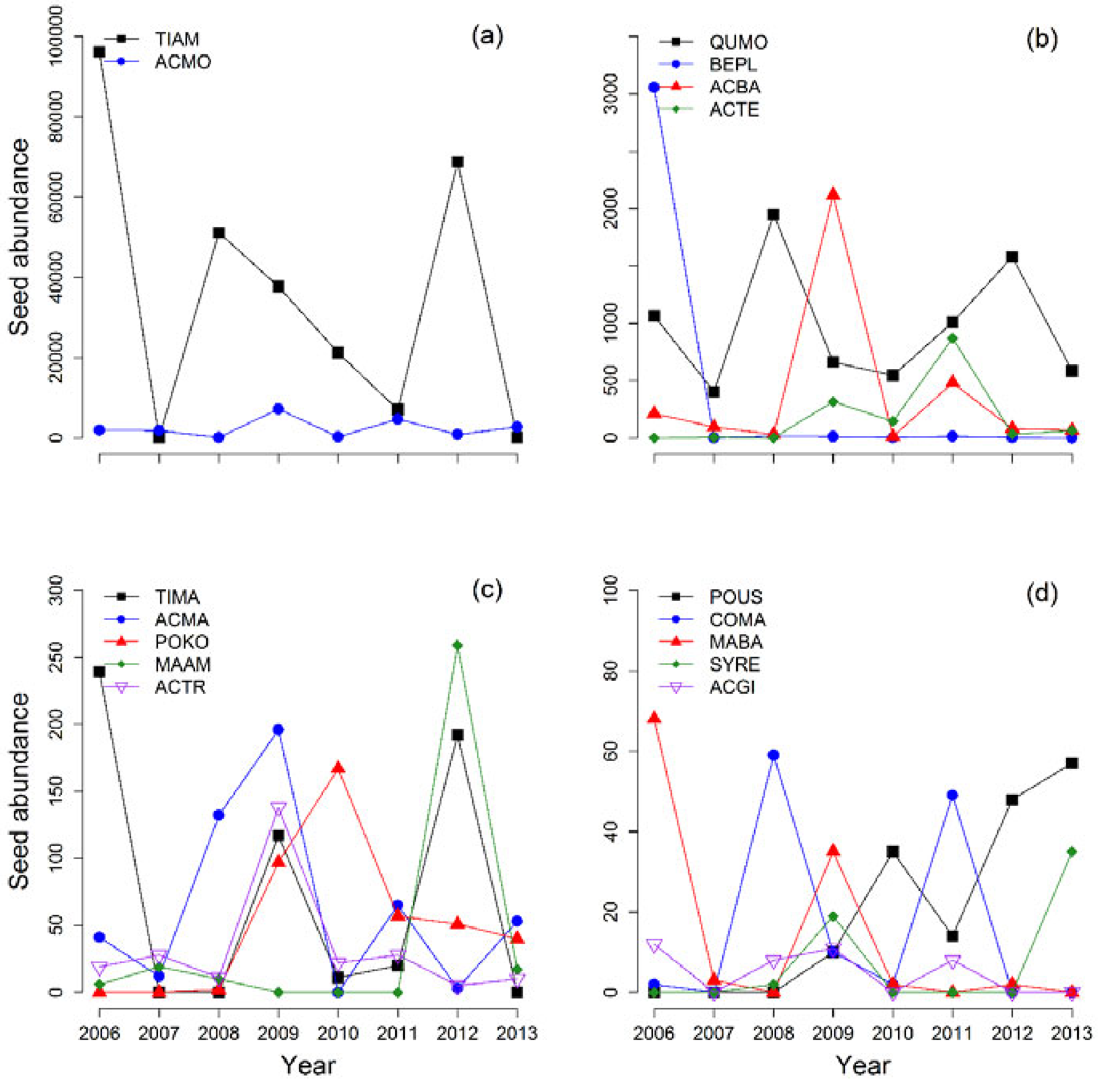

Figure 2 Annual seed production for the four species that met the filtering criteria (synchrony) and with $CV_{year} > 1$ in the order of descending seed abundance from 2006 to 2014 in the Changbaishan, China (left panels). The dashed line represents the long-term mean seed production during the study. Filled squares represent mast seeding years for each species, and open dots are non–mast years. The full names of these species can be found in Table1.

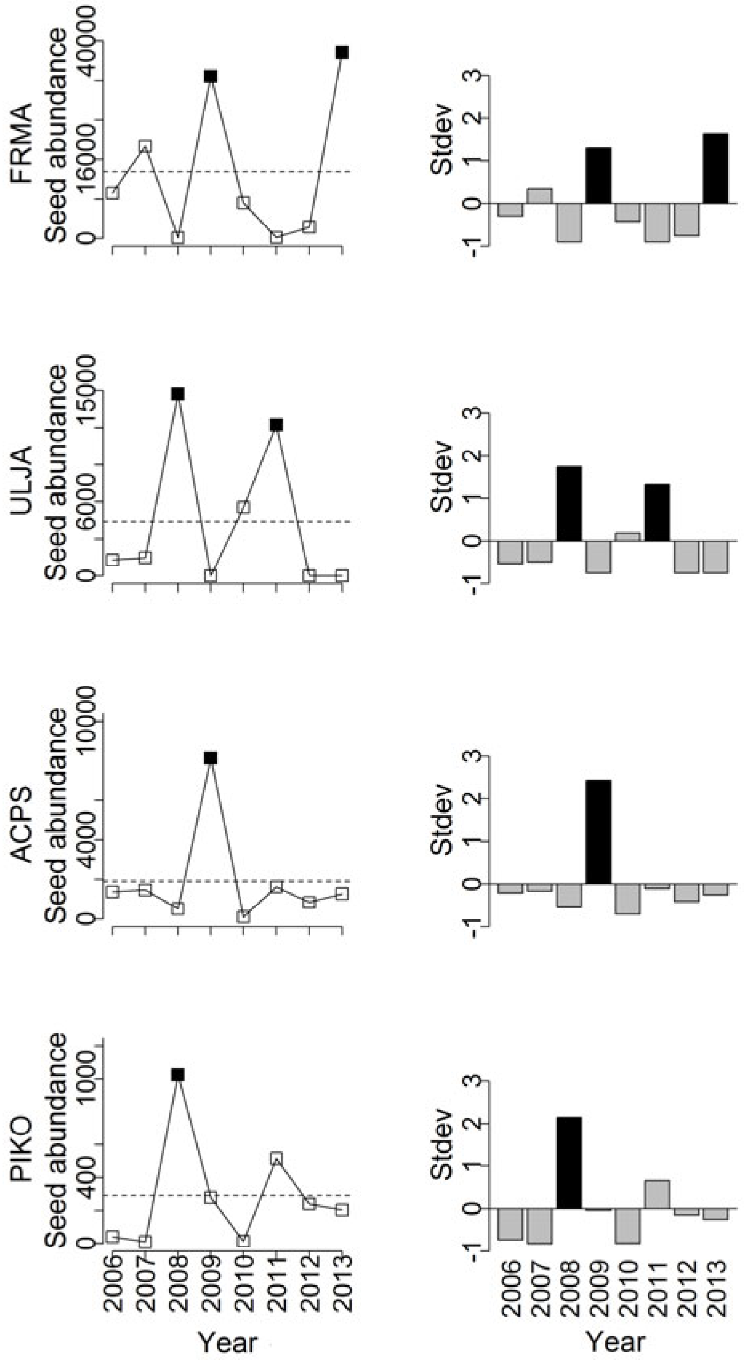

Figure 3 Mean (± SD) interannual variation of seed production (CV_{year}) weighted by seed abundance, for dispersal mode (**a**) and pollination vector (**b**) of 20 studied species. Significant differences of mean CV_{year} between vectors within each of these three reproductive traits are indicated by different letters (ANOVA weighted by seed abundance of each species, $P < 0.05$).