

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

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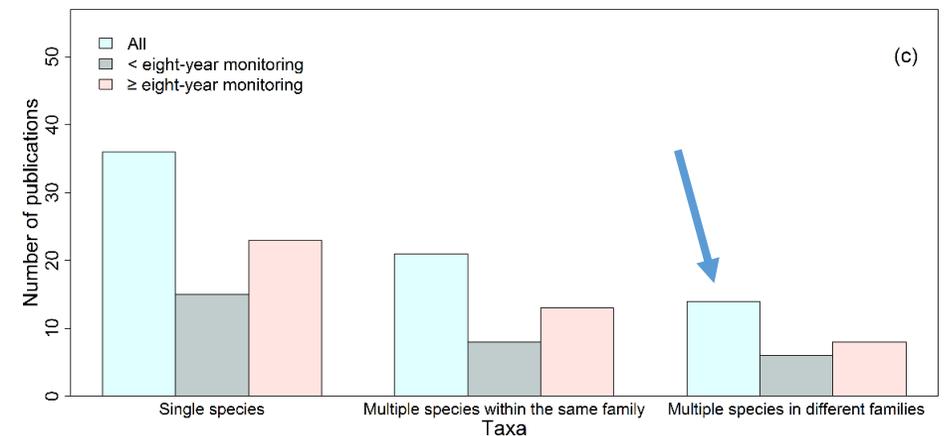
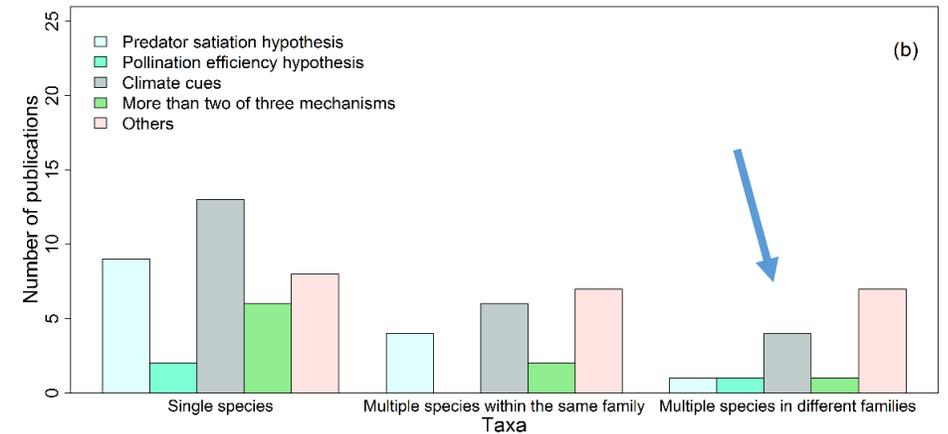
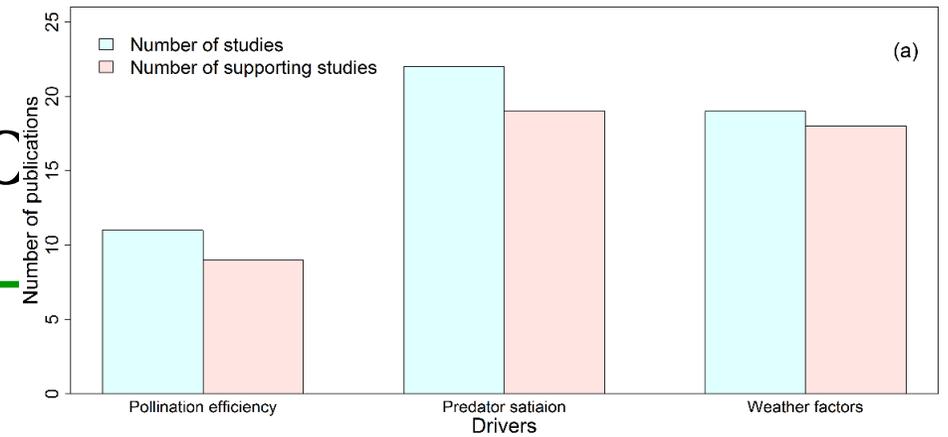
# Introduction

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- 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).
- Two predominant ultimate hypotheses for mast seeding are pollination efficiency and predator satiation, with weather conditions as a proximate cause (Kelly & Sork 2002).
  - Pollination efficiency: mast seeding should be strongly favored in plant species that achieve greater pollination efficiency through synchronized above-average flowering efforts (Nilsson & Wästljung 1987; Kelly & Sork 2002).
  - Predator satiation: large intermittent seed crops can benefit predator-dispersed plants by improving the chances of seeds escaping predation during a mast year (Janzen 1971; Kelly 1994; Vander Wall 2002; Fletcher et al. 2010).

# Introductio

- However, 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).
- Community-wide observations of seed production are rare (Yasaka et al. 2008; Chang-Yang et al. 2015).
- 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; Chang-Yang et al. 2015)



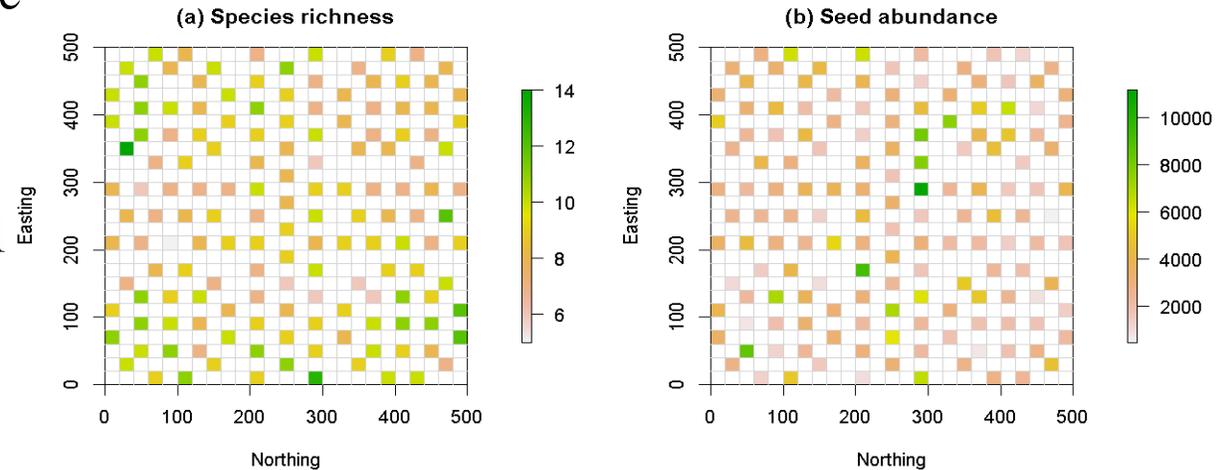
# Introduction

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- In this study, using an eight-year collection of seed trap data, we tested the pollination efficiency and predator satiation hypotheses and examine how weather conditions influence seeding variability.
- We predicted that:
  - 1) wind-pollinated species had more synchronous and intermittent seed crops over time than animal-pollinated species;
  - 2) predator-dispersed species had a higher interannual variation of seed production than species dispersed by abiotic modes, such as wind and gravity;
  - 3) changes in temperature and precipitation were associated with temporal variation of seed production;

# Materials: study area and data

- 25-ha ( $500\text{ m} \times 500\text{ m}$ ) Changbaishan temperate forest dynamic plot ( $42^\circ 23' \text{ N}$ ,  $128^\circ 05' \text{ E}$ ) in Northeast China
- 150 seed traps were set up in a relatively regular pattern and each trap was  $0.5\text{ m}^2$  ( $0.71\text{ m} \times 0.71\text{ m}$ )
- Eight years (from May 2006 to April 2014) of mature seed production of each species falling into all 150 traps.
- We used a subset of the database consisted of species fewer than 30 seeds across eight years (most of them came from only one or two seed traps) and a total of 20 species
- Reproductive traits (pollination vector and dispersal mode)
- Weather data (2005~2014)



# Methods: statistical analyses

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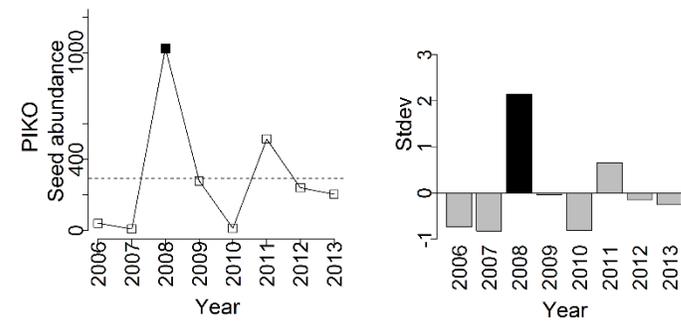
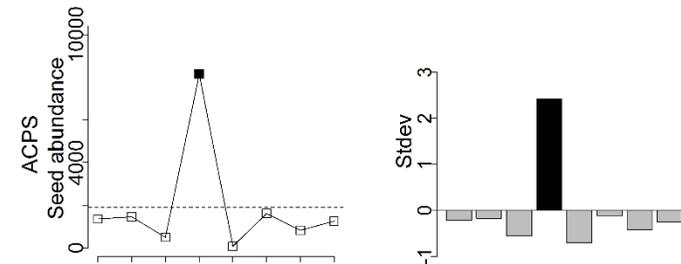
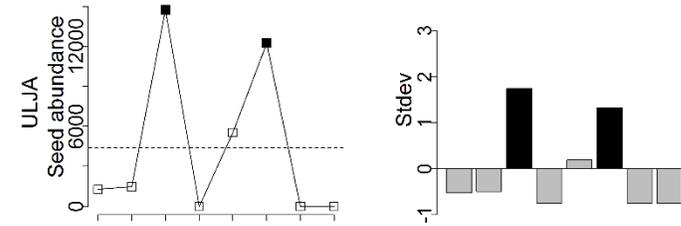
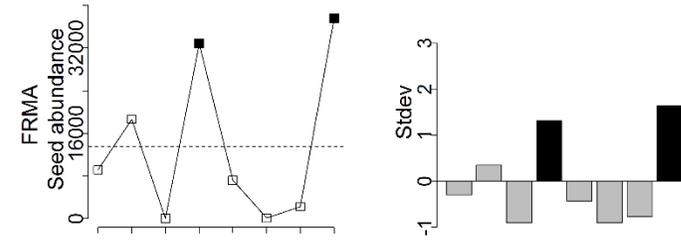
- *Variability in annual seed production* (coefficient of variation -  $CV_{\text{year}}$ )
- *Criteria of mast-seeding year* (yearly seed production — a standardized deviate (SD; mast year was defined as positive SD and beyond the range of the negative SD), LaMontagne & Boutin 2009)
- In assessing *mast-seeding patterns*, we excluded both the species that occurred in fewer than five seed traps and traps that had fewer than 100 seeds caught during eight-year period and *Pinus koraiensis*
- *Synchrony*: Spearman correlations were used for all pairwise comparisons of species
- *Testing two selective hypotheses: ANOVA*
- Effects of weather conditions: generalized linear mixed-effects model (GLMM); several species with more than 5,000 seeds

# Results: variability

Species name	Species code	Total seed abundance	Mean CV <sub>year</sub>	Dispersal mode	Pollination vector	Fruit type
<i>Tilia amurensis</i>	TIAM	282,115	0.991	Gravity	Insect	Fleshy
<i>Fraxinus mandshurica</i>	FRMA*	108,065	1.093	Wind	Insect	Dry–indehiscent
<i>Ulmus japonica</i>	ULJA*	35,277	1.345	Wind	Wind	Dry–indehiscent
<i>Acer mono</i>	ACMO	19,517	0.990	Wind	Wind and Insect	Dry–indehiscent
<i>Acer pseudo–sieboldianum</i>	ACPS*	15,250	1.421	Wind	Wind and Insect	Dry–indehiscent
<i>Quercus mongolica</i>	QUMO	7,792	0.560	Animal	Insect	Dry–indehiscent
<i>Betula platyphylla</i>	BEPL	3,100	2.781	Wind	Wind	Dry–indehiscent
<i>Acer barbinerve</i>	ACBA	<b>480,528</b>	1.849	Wind	Insect	Dry–indehiscent
<i>Pinus koraiensis</i>	PIKO*	2,327	1.970	Animal	Wind	Dry–indehiscent
<i>Acer tegmentosum</i>	ACTE	1,431	1.670	Wind	Wind and Insect	Dry–indehiscent
<i>Tilia mandshurica</i>	TIMA	579	1.345	Gravity	Insect	Fleshy
<i>Acer mandshuricum</i>	ACMA	502	1.098	Wind	Insect	Dry–indehiscent
<i>Populus koreana</i>	POKO	414	1.116	Wind	Wind	Dry–dehiscent
<i>Maackia amurensis</i>	MAAM	311	2.296	Gravity	Insect	Dry–dehiscent
<i>Acer triflorum</i>	ACTR	261	1.330	Wind	Wind and Insect	Dry–indehiscent
<i>Populus ussuriensis</i>	POUS	164	1.123	Wind	Wind	Dry–dehiscent
<i>Corylus mandshurica</i>	COMA	122	1.593	Animal	Wind	Dry–indehiscent
<i>Malus baccata</i>	MABA	110	1.814	Animal	Insect	Fleshy
<i>Syringa reticulata</i>	SYRE	58	1.869	Wind	Insect	Dry–dehiscent
<i>Acer ginnala</i>	ACGI	39	1.104	Wind	Insect	Dry–indehiscent

# Results: mast seeding

- All four species used to do mast analyses has been undergoing mast seeding during 2006-2014.
- ACPS and PIKO had one mast year during the period of the study, FRMA and ULJA had two mast years.

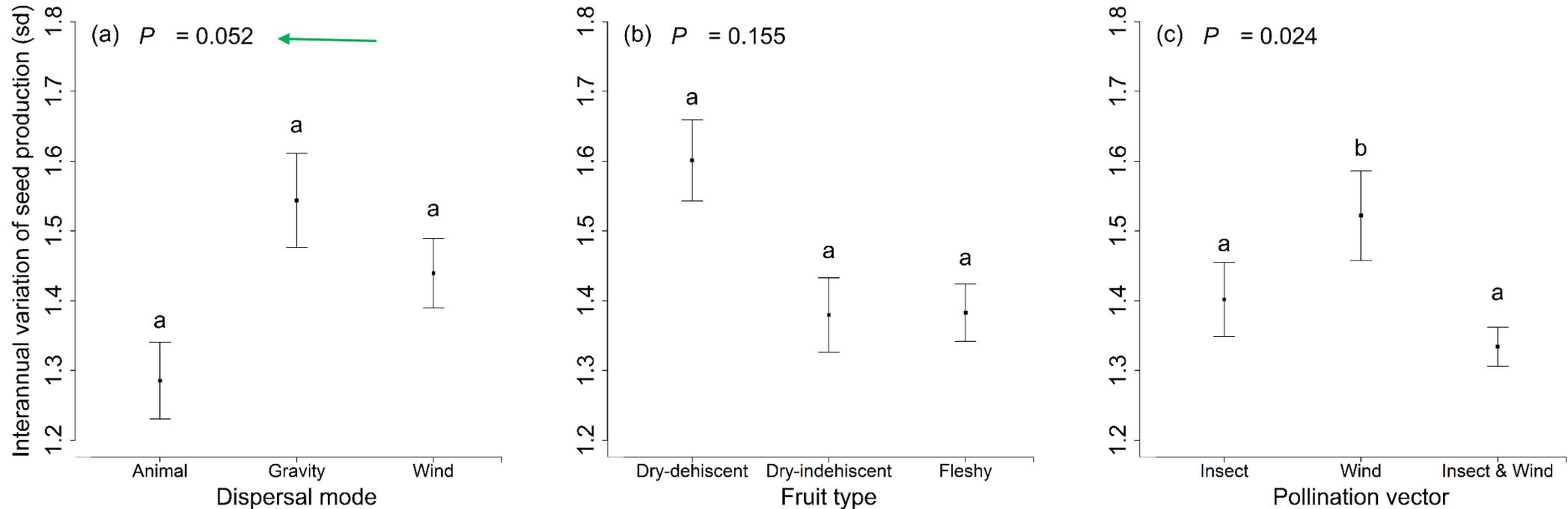


# Results: synchrony

	ACBA	ACPS	ACTR	ACGI	BEPL	ACMA	SYRE	PIKO	ULJA	TIMA
COMA	-	-	-	-	-	-	-	0.914 **	0.938 ***	-
QUMO	-	-	-	-	-	-	-	0.756 *	-	-
ULJA	-	-	-	-	-	-	-	0.796 *	-	-
ACPS	0.986 ***	-	-	-	-	-	-	-	-	-
ACTR	0.980 ***	0.975 ***	-	-	-	0.746 *	-	-	-	-
ACMO	-	0.880 **	0.833 *	-	-	-	-	-	-	-
MABA	-	-	-	0.707 *	0.880 **	-	-	-	-	-
FRMA	-	-	-	-	-	-	0.877 **	-	-	-
TIAM	-	-	-	-	-	-	-	-	-	0.862 **

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 and the seven *Acer* species showed poor synchrony.

# Results: testing hypotheses



For the pollination efficiency hypothesis, wind-pollinated species had a significantly higher mean  $CV_{\text{year}}$  than either animal-pollinated species or the species pollinated by both wind and animals

With respect to the predator satiation hypothesis, the weighted ANOVA showed that the mean  $CV_{\text{year}}$  was marginally significantly different among dispersal modes.

# Results: predation satiation

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- 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).
- Seed availability during some 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).
- Asynchronization among the four predator-dispersed species may reflect inconsistencies among plant genera or species in the relative magnitude of the advantages and disadvantages derived from community-wide patterns of seed production (Herrera et al. 1998).
- The composition of fruit and seed traits among co-fruiting (co-seeding) plants may also mediate competition or facilitation between plants for seed dispersers in a community (Razafindratsima & Dunham 2016).

# Results: weather drivers on seed production

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***		

Weather factors during spring flowering and seed ripening had significant effects on seed production for six of the seven focal species.

Species varied their responses to similar weather conditions.

Lag effects were also significant for some species, while the current spring phenology had a stronger effect on seed production than both the weather conditions of the current summer and season-long lags.

# Results: weather drivers on seed production

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- Interannual fluctuations in seed production indicates 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).
- The strong correlations between seed production and weather conditions suggests that weather triggers the variation and synchrony in mast seeding (McKone, Kelly & Lee, 1998; Schauber *et al.* 2002; Smail *et al.* 2011).
- Seasonal variation in temperate or rainfall can also mediate temporal fluctuations in phylogenetic pattern of phenology (e.g. seed production) in a community (Razafindratsima & Dunham 2016).

# Summary

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- Our findings suggest that pollination efficiency hypothesis had a much stronger effect than predation satiation hypothesis on mast seeding;
- 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 at both population and community levels.

***Thank you !***