

Biogeography and phylogeny of masting: do global patterns fit functional hypotheses?

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Summary

- Interannual variability of seed crops (CVp) has profound consequences for plant populations and food webs, where high CVp is termed ‘masting’. Here we ask: is global variation in CVp better predicted by plant or habitat differences consistent with adaptive economies of scale, in which flower and seed benefits increase disproportionately during mast years; or by passive mechanisms, in which seed production responds to variation in resource availability associated with climate variability?
- To address this question, we compiled a dataset for phylogenetic comparative analysis of long-term fruit/seed production for plants comprising 920 time series spanning 311 plant species.
- Factors associated with both adaptive benefits of CVp (wind pollination and seed dispersal) and climatic variability (variability of summer precipitation) were among the best predictors of global variation in CVp. We observed a hump-shaped relationship between CVp and latitude and intermediate phylogenetic and geographic signals in CVp.
- CVp is patterned nonrandomly across the globe and over the plant tree of life, where high CVp is associated with species benefiting from economies of scale of seed or flower production and with species that experience variable rainfall over summer months when seeds usually mature.

Introduction

Long-lived plants produce different sized seed crops from year to year. Plant taxa that have high interannual variation in seed crop for individuals within a population (CVi) as well as high synchrony among individuals within a population (S) are known as masting or mast-seeding species (Kelly & Sork, 2002; Koenig *et al.*, 2003; Pearse *et al.*, 2016). High S and CVi of seed crops lead to population-level interannual variation in seed set (CVp), which is important because it drives variation in animal populations and has effects that cascade through ecosystems (Jones *et al.*, 1998; Ostfeld & Keesing, 2000).

Studies from several plant systems have made rapid progress in uncovering the adaptive benefits of high CVp as well as the proximate mechanisms that drive high CVp (Norton & Kelly, 1988; Kelly & Sork, 2002; Crone *et al.*, 2009; Turnbull *et al.*, 2012; Kelly *et al.*, 2013; Miyazaki *et al.*, 2014; Pearse *et al.*, 2014, 2016). It is widely recognized that variation in the adaptive benefits of masting and the factors that affect proximate mechanisms of masting are both important to understanding which plants produce mast seed crops. Given these advances, there is a need to synthesize studies of long-term seed set in order to assess the degree to which global patterns in CVp are explained by variation

in adaptive benefits of variable seed set and variation in mechanistic constraints of seed production (Pearse *et al.*, 2016).

Adaptive benefits of high CVp

High CVp comes at an inevitable demographic cost, because a plant foregoes reproduction in some years (Waller, 1979). Because of this, it is thought that masting conveys adaptive benefits that compensate for those demographic costs. The adaptive benefits of variable and synchronous seed set are mainly attributable to ‘economies of scale’, in which the value of each flower or seed increases during mast seeding events (Norton & Kelly, 1988; Kelly & Sork, 2002). Selection due to these economies of scale in seed set is thought to be a major driver of high CVp, and variation in these selection pressures may lead to differences in CVp among species or populations (Kelly & Sork, 2002) by at least two mechanisms.

First, predator satiation may act as an economy of scale in seed set, where *per capita* survival of seeds is lower in years with higher reproductive effort (Janzen, 1971). High CVp in seed resources may be difficult for seed predator populations to track, thereby suppressing their populations during low seed years. However, this type of suppression may not be observed in habitats where

alternate resources such as other seed crops allow predator populations to remain high in low seed set years (Koenig & Haydock, 1999). Furthermore, predator satiation may be disadvantageous for plants whose dispersal or successful germination relies on seeds being harvested, and in some cases passed through the guts, of seed eaters.

Second, pollination efficiency may act as an economy of scale on flowering effort and thus seed set, where pollination success is higher in years with larger flowering effort (Norton & Kelly, 1988). Again, high CVp in flowering effort may be disadvantageous for plants with specialized pollinators if high CVp suppresses pollinators that rely on that species' inflorescences in years of low flowering. This potential limitation is less likely to be found in wind pollinated species (Herrera *et al.*, 1998; Kelly *et al.*, 2001; Kelly & Sork, 2002; Wang *et al.*, 2017). Likewise, insect pollination is spatially directed, so typically would not achieve efficiency gains by aggregating flowering effort into fewer larger years (Kelly *et al.*, 2001).

Proximate mechanisms driving CVp

Plants with high CVp tend to respond to interannual variation in weather such as temperature (Koenig *et al.*, 1996; Schaubert *et al.*, 2002; Krebs *et al.*, 2012; Pearse *et al.*, 2014; Roland *et al.*, 2014; Bogdziewicz *et al.*, 2018b), differences in temperature among years (Kelly *et al.*, 2013), or rainfall (Perez-Ramos *et al.*, 2010). While some plant clades or floras appear to respond similarly to weather, others exhibit individualistic or variable responses. For example, many plants in New Zealand respond to differences in summer temperatures (Kelly *et al.*, 2013), whereas seed set in different oak species appears to respond to disparate aspects of weather (Koenig *et al.*, 2016).

In addition to a relationship with weather, resource dynamics are thought to play an important role in determining seed set in plants with high CVp (Isagi *et al.*, 1997; Sala *et al.*, 2012). The availability of internal resources such as nutrients correlates with seed set in some species (Smaill *et al.*, 2011; Tanentzap *et al.*, 2012; Miyazaki *et al.*, 2014) and depletion of resources helps to explain lagged negative autocorrelations in seed set that are commonly observed in time series of masting species (Pearse *et al.*, 2016). Accordingly, plants growing in resource-limited habitats tend toward higher CVp (Smaill *et al.*, 2011; Tanentzap *et al.*, 2012; Barringer *et al.*, 2013; Fernandez-Martinez *et al.*, 2019), resulting in a negative relationship between long-term fecundity and interannual variation in fecundity (Pesendorfer *et al.*, 2016; Pearse *et al.*, 2017).

Large scale patterns of CVp

A key insight from past syntheses of seed set in long-lived, iteroparous plants has been that plants show continuous variation in CVp, making it impossible to delimit 'masting' as a unique reproductive strategy (Kelly, 1994; Herrera *et al.*, 1998; Koenig & Knops, 2000). This wide variation in CVp is driven by the interaction of plants with their environments (Kelly & Sork, 2002; Tanentzap *et al.*, 2012; Kelly *et al.*, 2013; Koenig *et al.*,

2016; Monks *et al.*, 2016). Thus, the spectrum of CVp observed among long-lived plants can be understood as a consequence of overlapping processes: *environmental response*, whereby plants growing in a particular environment have a high CVp because of factors that inhibit or promote seed set in some years; *evolutionary adaptation*, whereby high CVp evolves due to the adaptive advantages imparted by economies of scale associated with pulsed, synchronous seed set; and *evolutionary conservatism*, whereby close relatives tend to have similar CVp. Previous reviews have considered only a subset of these hypotheses (Herrera *et al.*, 1998; Kelly & Sork, 2002). Moreover, because research has largely focused on adaptive explanations of variation in CVp among plant species, there is a need to assess adaptive explanations of CVp while simultaneously considering factors associated with environmental variation in order to disentangle the role of these processes in determining variation in CVp across the plant tree of life (Kelly, 1994).

The literature on seed set CVp has historically focused on economically important Northern Hemisphere forestry trees and masting species whose variable seed crops determine fluctuations in economically important animal populations (Herrera *et al.*, 1998). More recently the scope of studies on interannual variation in seed crops has increased, with large surveys of seed set across a wide variety of plant taxa across the globe (Fig. 1; Supporting Information Fig. S1). Here we use a global dataset of seed set CVp to assess support for predictions about patterns in CVp among taxa. Our goal is to determine the degree to which predictors of CVp predicated on adaptive benefits and on environmental constraints explain global variation in CVp. Where possible, we test hypotheses about variation in CVp at both the interspecific and intraspecific scales using phylogenetically explicit comparative analyses and subject-centering, respectively.

Hypotheses and predictions

Several predictions can be made based on hypotheses for how CVp varies across the globe, among plant species, and among populations within a plant species.

Latitudinal gradient in CVp CVp is expected to increase with latitude for two reasons. First, because the diversity of tree species is low at high latitudes, predator satiation may be more effective at higher latitudes because there are fewer alternate resources for seed predators (Kelly & Sork, 2002; Wright *et al.*, 2005; Bogdziewicz *et al.*, 2016, 2018a). In this case, the interannual CV of seed production at the community level (CVc) is likely to reflect CVp of individual species to a greater degree at more poleward latitudes. Second, because wind pollination is more prevalent in temperate or more poleward latitudes than in tropical habitats characterized by high species richness, CVp may be greater at higher latitudes due to the benefits of CVp to the efficiency of wind pollination (Kelly *et al.*, 2001). This hypothesis is discussed further in the 'wind pollination' section below.

Masting associated with climate variation Years of high annual seed set are often associated with weather in the same or previous

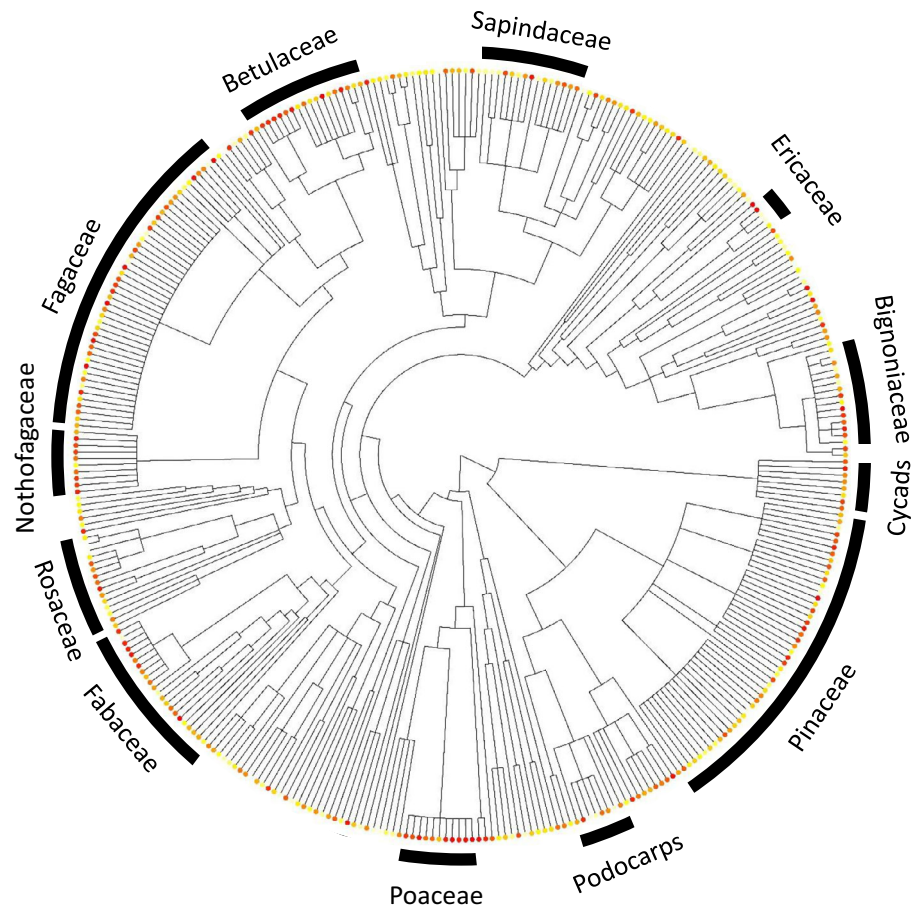


Fig. 1 CVp mapped onto a plant phylogeny. Warmer colors (reds) indicate higher CVp (range of 0.5–3.3). Taxonomic groupings of plants with many CVp records are shown.

years. If weather limits seed set in some years but not others (Koenig *et al.*, 2015; Bogdziewicz *et al.*, 2018b), then greater interannual variability in weather should translate into greater CVp. Two aspects of weather have emerged multiple times as correlates of seed set, likely because of their close connection to the process of seed production. Summer droughts may limit the ability of plants to produce seed crops while maintaining other functions (Perez-Ramos *et al.*, 2010; Wion *et al.*, 2019), and years with high spring temperatures may result in increased pollination (Bogdziewicz *et al.*, 2018b) or act as a general cue for reproduction (Kelly *et al.*, 2013).

Resource limitation or autocorrelation Many masting species display a pattern of negative lag-1 autocorrelation in seed set, such that two large seed years rarely occur one after another (Sork *et al.*, 1993; Koenig *et al.*, 1994). Resource budget models suggest that such negative autocorrelation is caused by resource limitation following a large seed crop, and that a larger ‘threshold’ of resources needed for a full seed crop relative to the resources accumulated in a given year is a property of masting species with high CVp (Isagi *et al.*, 1997; Crone & Rapp, 2014). Consistent with this idea, lagged dynamics in seed production are associated with plant species with low nutrient levels (Fernandez-Martinez *et al.*, 2019). Thus, to the extent that a greater lag-1 negative autocorrelation is a proxy for resource limitation – which is likely, but not necessarily the case (Kelly *et al.*, 2013) – we expect

higher CVp in plants that exhibit greater lag-1 negative autocorrelation in seed production.

Wind pollination CVp should be higher in plants that are wind pollinated than those that are animal pollinated because CVp may increase pollination efficiency in wind pollinated plants but potentially saturates pollination efficiency in plants that rely on specialized animal pollinators (Herrera *et al.*, 1998; Kelly & Sork, 2002; Wang *et al.*, 2017).

Seed dispersal mode CVp should be lower in plants, such as those with fleshy fruits, whose seeds are commonly passed through the gut of seed predators or dispersers. For other seed dispersal types (those not dispersed by animals or those dispersed by animals that eat and kill a portion of the seeds), high CVp can result in predator satiation and a higher survival rate of seeds (Herrera *et al.*, 1998).

Life form CVp may differ between life forms of plants (e.g. trees, shrubs, forbs, grasses) due to differing economies of scale or constraints associated with those life forms.

Phylogenetic conservatism This hypothesis proposes that CVp is similar among closely related species and can be explained by the evolutionary histories separating plant clades (Tanentzap & Monks, 2018).

We tested each of the above hypotheses by comparing CVp of 311 plant species with plant traits and environmental variability in a phylogenetic framework.

Materials and Methods

Compiling data

We employed four techniques to assemble records of interannual seed set with the goal of compiling a comprehensive list of seed/fruit set datasets. First, we searched Web of Science using combinations of search terms such as ‘interannual vari*’, ‘seed set’, ‘fruit set’, ‘masting’ and ‘seed crop’. Second, we scanned the references of each dataset to find additional records of seed set, and then searched references of every subsequent dataset found. Third, we contacted managers of forestry districts, wildlife surveys, and regional seed surveys to ask directly for access to their information on interannual variation in seed set. Finally, we solicited seed set datasets from scientists contacted through the ECOLOG listserv (<https://listserv.umd.edu/archives/ecolog-l.html>). Additional details can be found in Pearse *et al.* (2017).

Inclusion of a record in our database was contingent on several criteria. First, we only included records with six or more consecutive years of quantitatively determined seed set from a species at a given site. Second, records were only included if seed set could be assigned to plants of a particular species. Third, we excluded records that were measured in such an indirect way (such as via anticipated correlations with game abundance) that extraneous factors were likely to compromise their accuracy. Fourth, we only included records of fruit set, seed set, or inflorescence set – the last in cases where inflorescences are strong indicators of seed set. We excluded records of pollen production, because interannual variation in seed set often varies with pollen abundance (Norton & Kelly, 1988), although not in all cases (Perez-Ramos *et al.*, 2010). Fifth, we excluded records from agricultural settings because management practices could affect variation in crop sizes. Finally, we only included records from iteroparous perennial terrestrial plants whose interannual variation in seed set could not be explained by changes in population size.

We retained quantitative records of fruit or seed set with measurements including complete counts per individual, timed counts, and seed or fruit traps and funnels. Seed set was recorded in a variety of units, including counts per individual, timed (relative) counts per individual, counts per area, mass per area, volume per area, and seed energy (calories) per area.

This approach resulted in the inclusion of 920 records of seed set of 311 plant species (with 1–54 sites per species) from 205 studies. The studies in the database span the years 1900 to 2014. The dataset included all seed set records utilized in past reviews of seed masting (Silvertown, 1980; Herrera *et al.*, 1998; Koenig & Knops, 2000; Kelly & Sork, 2002) and resulted in an approximate two-fold increase in datasets from the largest previous meta-analyses of seed set (Koenig & Knops, 2000; Kelly & Sork, 2002).

Of all species included in the dataset, 35% were either Pinaceae (15%) or Fagaceae (20%). The average record length

was 13.1 yr, and 131 records were greater than 20 yr. Importantly, studies in the present dataset spanned many geographic regions, ranging from 69.7°N to 51.3°S and covered all six major vegetated continents (Fig. S1). As in prior syntheses, however, there were few records of seed set from Africa (17) and an abundance of records from temperate North America (385), Europe (258), Japan (53), New Zealand (64) and Central America (118).

Using these time series, we calculated CVp as the standard deviation divided by the mean seed set. CVp varied continuously and was unimodally distributed among seed set datasets (Fig. 2a), and among plant species (Fig. 2b). We estimated lagged autocorrelations (lag 1–lag 4) for time series of seed set using the *acf* function in R (R Development Core Team, 2016).

We compiled a dataset of nine climatic variables relating to interannual weather variability (coefficient of variation (CV) of mean annual, summer, and spring precipitation; SD of mean annual, summer and spring maximum and minimum temperatures). Climate records were associated with the site and time-frame of each seed set record using data from the Global Historical Climatology Network (Lawrimore *et al.*, 2011), accessed 15 July 2014. Data were recorded from the nearest weather station (median distance = 35 km; in the few cases ($n = 36$) in which weather stations were more distant than 500 km, weather data was considered missing. Summer variables were calculated for June–August for sites in the Northern Hemisphere and January–March for sites in the Southern Hemisphere; spring values were April–June in the Northern Hemisphere and September–November in the Southern Hemisphere. We compiled information on the life form (tree, shrub, liana or vine, and other, including forbs, grasses, and succulents), pollination type (animal or wind), and seed dispersal mode (endozoochorous, dyszoochorous, or nonzoochorous) at the species level from floras, natural histories, and past datasets (Herrera *et al.*, 1998; Kelly & Sork, 2002; Wright *et al.*, 2005).

We estimated phylogenetic relationships among plant taxa in the dataset by pruning a recent large-scale, ultrametric, time-calibrated phylogeny of seed plants (Zanne *et al.*, 2014) to the species in our dataset. Matches to genera and families were used in cases where species were not present in the seed plant phylogeny. The pruned phylogeny is presented in Pearse *et al.* (2017).

Statistical analysis

All analyses were conducted in R (R Development Core Team, 2016). We calculated Pagel’s lambda (λ) as a quantitative measure of phylogenetic signal of CVp, and we tested for significance of λ (deviation from a value of 0, indicating no phylogenetic signal) using a randomization test implemented using *phylosig* in the PHYTOOLS package (Revell, 2012).

To describe interspecific patterns in CVp, we condensed the full CVp dataset to species means of CVp, geographic location (latitude and longitude), climatic variables, and dataset length. Most categorical descriptors of datasets were invariant within species, with the exceptions of ‘site’ and ‘country’. The number

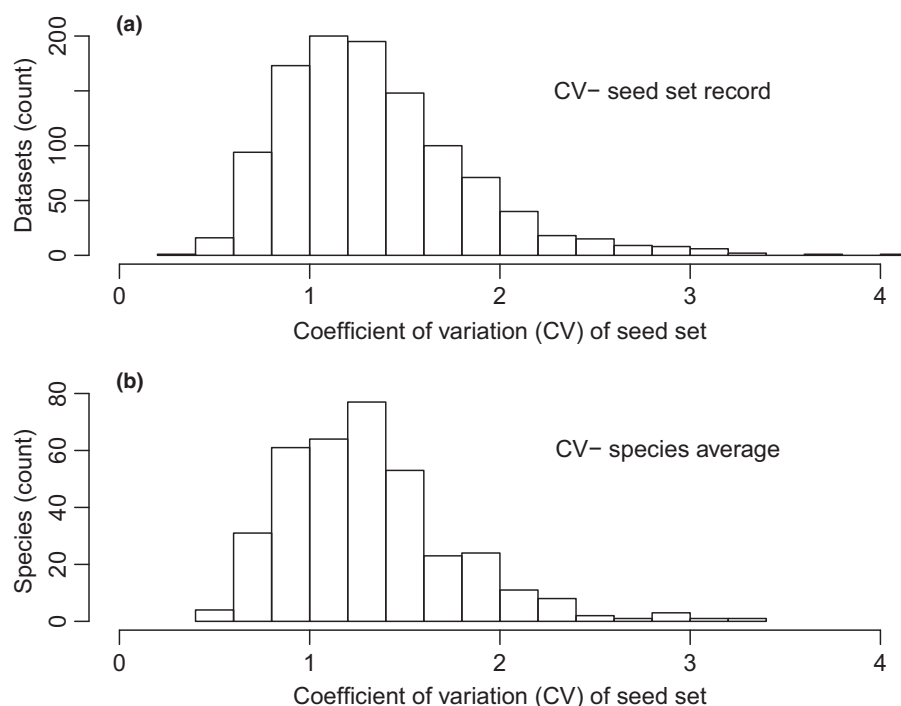


Fig. 2 Histograms of CVp among (a) all datasets ($n = 920$) and (b) mean CVp of each species ($n = 311$) have unimodal distributions, suggesting that masting (high CVp) is not a unique reproductive strategy.

of sites at which seed set of a species was observed did not correlate with CVp (Pearson $r = 0.03$, $df = 311$, $P = 0.54$), suggesting that CVp was not biased by species with more extensive sampling. Likewise, because CVp has increased within some time series in this dataset (Pearse *et al.*, 2017), we tested whether older time series had lower CVp, but we found no evidence for this (pGLS, $n = 311$, $t = 0.2$, $P = 0.82$). We considered ‘country’ to be the country with the most records of seed set, as it was uncommon for records within a species to be from multiple countries (only 23 (6%) of 363 species). We tested whether geographically close species had similar CVp values using a Mantel test to compare a distance matrix of species-level CVp with a Euclidean distance matrix of species mean geographic location.

We built a linear model of CVp including 14 total effects: pollination type, seed dispersal type, latitude, lag-1 autocorrelation, CV precipitation, CV spring precipitation, CV summer precipitation, SD annual max temperature, SD spring max temperature, SD summer max temperature, SD annual minimum temperature, SD spring minimum temperature, SD summer minimum temperature, and life form. Standard deviation was used to characterize variability in temperature because temperature ($^{\circ}\text{C}$) is not bounded at 0. A quadratic effect of latitude was included in the model to allow for nonlinear relationships between CVp and latitude (Kelly & Sork, 2002).

We estimated full models using phylogenetic generalized least squares (pGLS). We allowed models to estimate phylogenetic signal (λ) in the regression residuals and adjust tree length based on λ as described by Revell (2010) using the *corPagel* function in R package *APE* (Paradis *et al.*, 2004); this has the effect of optimizing a scaling factor on the off-diagonal elements of the covariance matrix for the regression residuals between the extremes of a multivariate normal distribution under a Brownian motion model at

one end, with no covariance – that is, no phylogenetic structure – at the other. This approach obviates the need to test both a phylogenetic and a nonphylogenetic regression, which is problematic because these are only endpoints of a model continuum. It also has the benefit of minimizing variance on the regression coefficients, because the GLS with an appropriate covariance matrix is the best linear unbiased estimator (Blomberg *et al.*, 2012). We reduced models in a two-step process. First, we calculated a corrected variance inflation factor (GVIF) that accounts for inflation of numerical and categorical model effects. We excluded predictors based on a squared GVIF value > 10 , and we present squared GVIF of full models in Table S1. When weather variables had high GVIF due to covariation with a conceptually similar predictor (e.g. annual mean maximum temperature and summer mean maximum temperature), we included annual weather estimates over seasonal estimates.

Next, we reduced this intermediate model based on small-sample Akaike information criterion (AICc) weights. We used the *dredge* function in the *MUMIN* package (Bartoń, 2009) in R to estimate AICc of models based on all combinations of model predictors. We used this to create a reduced model that included predictors that were present in any model within $\Delta\text{AICc} < 2$ from the model with the lowest AICc. We estimated R^2 based on the likelihood ratio estimate of the GLS model compared to a null GLS model with no predictors and with the same correlation structure (Nakagawa & Schielzeth, 2013).

We tested whether species that were close to each other in geographic space had similar CVp using a Mantel test on species means to compare similarity of CVp with geographic distance between species. Because latitudinal gradients have been observed in past studies (Koenig & Knops, 2000; Kelly & Sork, 2002; Wright *et al.*, 2005), we explored the effect of latitude on CVp in

a set of separate models. We explored whether there were differences in latitudinal gradients in CVp by either including the absolute value of latitude in models or latitude separated by hemisphere in two separate models. Finally, because tendencies toward wind pollination and certain seed dispersal mechanisms have been suggested as reasons why plants in temperate latitudes tend to have higher CVp, we tested the relationship between absolute latitude and pollination type (wind vs animal) as well as seed dispersal mode (endozoochorous vs other modes) using the binomial phylogenetically-corrected generalized linear model (GLM) function *phylglm* in R package *PHYLOLM* (Ho & Ané, 2014). Because the phylogenetically-corrected GLM did not converge for seed dispersal mode, we tested this relationship using a regular GLM with a binomial error distribution.

Intraspecific variation in CVp

We tested for within-species geographic effects of latitude and geographic site on CVp using subject-centered mixed models (van de Pol & Wright, 2009). For subject-centering, the CVp of each record was centered to the mean CVp for a species as $CVp_{(record)} - CVp_{(species\ mean)}$, thereby isolating within-species variation in CVp and eliminating between-species variation. We then asked whether subject-centered CVp was affected by site or latitude using a mixed model with subject-centered CVp as the response variable, length of dataset as a fixed effect, species as a random effect on the intercept, and either the absolute value of latitude as a fixed effect or site as an additional random effect on the intercept. For the 40 plant species that had records from six or more sites, we tested whether records from geographically close sites had similar values of CVp using Mantel tests.

Results

Economy of scale and variable climate as drivers of worldwide CVp

CVp varied based on plant traits that affect the consequences of masting for plant fitness, such as pollination type and seed dispersal mechanism (Tables 1, S1). CVp was also greater in plant species that grow in areas with more variable summer rainfall. However, contrary to expectations, CVp tended to be lower for species in habitats with more variable spring maximum temperatures, as well as in habitats with more variable summer and annual minimum temperatures. Thus, a combination of environmental variability and plant traits relating to economies of scale best explained global variation in seed set variability (CVp).

Phylogenetic signal and taxonomic patterns

CVp displayed an intermediate but statistically significant phylogenetic signal (Pagel's $\lambda = 0.21$; $P = 0.008$), consistent with some taxonomic groups having a greater propensity toward high CVp, along with frequent evolutionary origins of high CVp (Fig. 1).

Biogeographic patterns

Within species, we found mixed evidence for a geographic signal of seed crop variability. Of the 41 plant species whose seed set records were represented by 6 or more sites, 13 displayed a significant geographic signal in CVp based on Mantel tests, indicating that geographically closer sites tended to have similar CVp values (Table S2). The intraspecific geographic signal was greater for species with high average CVp ($pGLS$, $\chi^2 = 9.8$, $P = 0.002$), suggesting that species with a stronger tendency toward masting displayed more spatial signal in CVp than plants with relatively even seed production between years. We failed to detect any within-species latitudinal gradient in masting (subject-centered mixed model: $\chi^2 = 0.1$, $P = 0.72$).

Among species, CVp varied considerably over space. Species that were geographically close to one another had more similar CVp than expected by chance (Mantel test: $r = 0.13$, $n = 363$, $P = 0.001$). We also found a latitudinal trend in masting among species (Table 1; Fig. 3). CVp reached a maximum in species at absolute latitudes of roughly 40° (Table 1; Fig. 3a), with a quadratic (hump-shaped) effect driven by Northern Hemisphere records. When the dataset was reduced only to Northern Hemisphere species, we found the same hump-shaped relationship between CVp and latitude ($pGLS$; Latitude (linear): $t_{269} = 3.3$, $P = 0.001$, Latitude (quadratic): $t_{269} = -3.1$, $P = 0.002$, Fig. 3b). In the Southern Hemisphere, CVp had no significant linear relationship with latitude ($pGLS$; Latitude (linear): $t_{54} = -1.1$, $P = 0.25$, Fig. 3b). The difference between latitudinal trends in CVp in the Northern vs Southern Hemispheres likely reflects a

Table 1 Fit of reduced model explaining CVp of seed set at the global scale.

Reduced global model			
Parameter	df	χ^2 (sign)	Standard slope (SE)
Latitude (lin)	1	15.6	0.03 (0.007)
Latitude (quad)	1	4.4	-0.0002 (0.0001)
Pollination type	1	5.9	*
Seed dispersal	2	10.8	*
Life form	3	—	—
lag-1 autocorrelation	1	—	—
CV annual precipitation	1	—	—
CV spring precipitation	1	—	—
CV summer precipitation	1	5.4	0.07 (0.03)
SD max annual temperature	1	—	—
SD max spring temperature	1	5.1	-0.12 (0.05)
SD max summer temperature	1	—	—
SD min annual temperature	1	3	-0.10 (0.06)
SD min spring temperature	1	—	—
SD min summer temperature	1	4.4	-0.09 (0.04)
$R^2 = 0.21$			

PGLS models were constructed to take into account similarities among closely related species. Marginal effects of variables were calculated with a Wald (χ^2) test, and standardized slope coefficients ($\pm$ SE) are shown. CV, coefficient of variation among years; SD, SD among years. Predictors dropped from reduced models are marked with a dash (—). Slopes coefficients were calculated for categorical variables marked with an asterisk (*).

truncation of forested land masses at southern latitudes at around 50°S and a smaller sample size of datasets in the Southern Hemisphere, particularly in equatorial latitudes.

We tested whether latitudinal variation in plant functional characteristics (pollination type and seed dispersal mechanism) mirrored latitudinal variation in CVp. Wind pollination was more common in temperate habitats (binomial pGLM, $df=309$, positive linear effect of latitude, $z=4.9$, $P<0.001$; quadratic effect, $z=-1.3$, $P=0.18$). Likewise, plants with seed dispersal modes that benefit from predator satiation (nonzoochory and dyszoochory) are over-represented at higher latitudes (binomial GLM, $df=309$, positive linear effect of latitude, $t=4.9$, $P<0.001$). However, in a model that included pollination type and seed dispersal mode as well as latitude, each explained variance in CVp (Table 1), suggesting that the latitudinal gradient in CVp is not entirely caused by differences in pollination and seed dispersal type among latitudes.

Temporal autocorrelation and functional differences

Across all seed set datasets, we observed significant lag-1 negative autocorrelations (mean lag-1 ACF = -0.19 , $P<0.001$, Fig. 4a). We hypothesized that species with greater CVp would have more negative lag-1 autocorrelations in seed production, but we found no evidence for this (Table 1). Instead, we observed a hump-shaped relationship between lag-1 autocorrelations and CVp, such that species with high CVp had a more consistent and slightly negative lag-1 autocorrelation than did species with low

CVp (Fig. 4b, quadratic effect of lag-1 autocorrelation, $t=-5.1$, $P<0.001$).

CVp varied based on plant traits associated with economies of scale of seed production. In line with expectations, CVp was greater in plant species that were wind pollinated as opposed to animal pollinated (Fig. 5). CVp was lower in plant species with endozoochory seed dispersal (seeds that are commonly passed through the gut of animals) compared to plants with seeds that are either wind dispersed (nonzoochory) or dispersed by animals that consume and kill seeds (dyszoochory) (Fig. 5). Shrubs and plants with 'other' life forms (forbs, grasses, and succulents) that were grouped together because of a paucity of records tended to have higher CVp than trees and lianas (Fig. 5).

Discussion

Global variation in CVp among plant species was related both to factors that reflect the potential adaptive benefits of masting, such as pollination and seed dispersal type, as well as factors that might reflect how a plant responds to a variable environment, such as variation in summer rainfall. This suggests that, across the plant tree of life, CVp of land plants is tied to both life history characteristics and weather.

Consistent with previous taxonomic analyses (Kelly, 1994; Herrera *et al.*, 1998; Kelly & Sork, 2002), we found that CVp was unimodally distributed. We observed a modest phylogenetic signal in CVp that was mostly caused by similarity in CVp among congeneric plants rather than consistency of CVp at higher taxonomic levels (Fig. 1, Tanentzap & Monks, 2018). Because there have been relatively frequent transitions between low and high CVp over the plant tree of life, our analyses suggest that CVp tends to evolve repeatedly in concert with transitions to wind pollination, certain types of seed dispersal, and environments with variable summer rainfall.

Also, consistent with past studies (Herrera *et al.*, 1998; Kelly & Sork, 2002), our study points to a tendency toward high CVp in wind pollinated species. This supports the pollination efficiency hypothesis (Norton & Kelly, 1988) as a major selective advantage of masting. Likewise, our analysis showed a strong connection between seed dispersal mechanism and CVp as would be anticipated by the predator satiation hypothesis. CVp because of plant species with seed dispersal by animals that pass seeds through their guts (endozoochory) tend to have the lowest average CVp. Seed dispersal mechanism is somewhat tied to pollination mechanism in our dataset, in which there are only 19 examples of species with wind pollination and endozoochory, so teasing apart pollination and seed dispersal effects on CVp is difficult.

Our study does not provide a test of the environmental prediction hypothesis, which suggests that variable seed production may enable plants to allocate seed production to years with favorable conditions for seedlings. This idea has gained recent support due to the effect of large-scale climatic teleconnections on both seed production and events that affect seedling survival (Ascoli *et al.*, 2020).

Plant species that live in environments with more variable summer rainfall had greater CVp, but no other aspects of weather

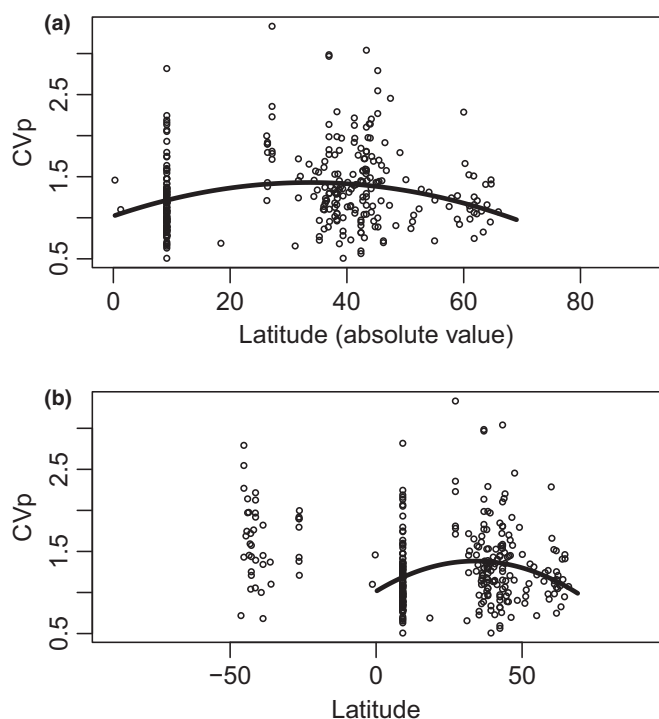


Fig. 3 Latitudinal gradient in CVp. (a) In combination, northern and southern datasets show a hump-shaped (quadratic) relationship between CVp and (absolute value) latitude ($n=311$ species). (b) A hump-shaped relationship between CVp and latitude occurs in the Northern Hemisphere.

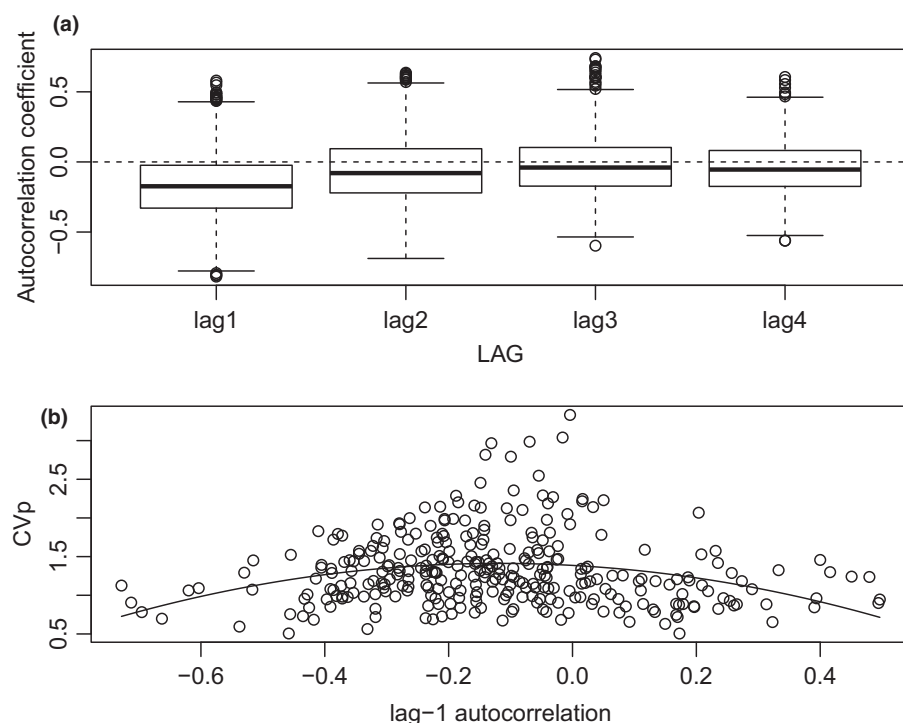


Fig. 4 Temporal autocorrelation in population level seed set by species ($n = 311$). (a) Prominent negative lag-1 autocorrelation was found in the majority of seed set time series. Longer scale autocorrelations (lag-2 through lag-4) tended to be negative, though not as prominent. Boxes show medians and 1st and 3rd quantiles, and whiskers are set at $1.5 \times$ interquartile range. (b) Population-level lag-1 autocorrelation was not related to population-level seed set variation (CVp).

variability resulted in higher CVp. Summer rainfall is often implicated in interannual differences in seed production, particularly in water-limited environments (Perez-Ramos *et al.*, 2010; Wion *et al.*, 2020). We found no evidence that high CVp was a consequence of variation in spring temperatures, as suggested by pollination ‘vetos’ during years of late springs, or frosts (Koenig *et al.*, 2015; Bogdziewicz *et al.*, 2018b).

We found that lagged, negative autocorrelations were ubiquitous properties of seed set in long-lived plants (Fig. 4). Two hypotheses have been proposed to explain this pattern. First, resource budgets might cause lagged autocorrelations in seed production if large seed set events consume more resources than can be produced in a year, and multiple years are needed to accumulate resources up to some threshold necessary to initiate the next reproductive event (Isagi *et al.*, 1997). In the classic resource budget model, we would expect that as lag-1 autocorrelations become more negative, CVp would increase. Our analysis did not support this. Alternatively, differential weather cues (where plants reproduced based on the difference in temperature across years) may drive lag-1 autocorrelations in seed production (Kelly *et al.*, 2013).

These alternatives are difficult to differentiate (Pearse *et al.*, 2014; Holland & James, 2015; Monks *et al.*, 2016). To date, the only known correlate of lag-1 autocorrelation of seed set among plant species is low nutrient concentration and imbalanced composition of nutrients in vegetative tissues (Fernandez-Martinez *et al.*, 2019), a trait likely associated with resource dynamics. It remains an unanswered question why plants with a high CVp have a constrained and intermediate, negative lagged autocorrelation, while plants with low CVp may have a wide range of lagged autocorrelations.

CVp of seed set was not randomly distributed across the globe. Species and individual populations that were closer to one another had more similar CVp than those that were far apart. One large-scale CVp pattern, previously found by Kelly & Sork (2002), was a unimodal latitudinal gradient in which CVp peaked for plants in the temperate regions at roughly 40°N and 40°S (Fig. 3). This pattern persisted when accounting for phylogenetic relationships among plant species, which, in combination with the relatively low but still significant values of λ we observed for CVp, suggests that during repeated transitions among latitudes, masting has evolved in parallel in clades inhabiting temperate latitudes. Because wind pollination is also more common at temperate latitudes, part of this latitudinal trend in CVp can be attributed to transitions to wind pollination. However, because wind pollination and latitude accounted for a sizable proportion of variation in CVp in a multiple regression models (Table 1), we conclude that transitions to wind pollination do not account for all of the latitudinal gradient in CVp.

The rapid accumulation of long-term data on plant reproduction increasingly allows us to understand the spatiotemporal patterns of seed production and to hint at processes that may govern those patterns (Herrera *et al.*, 1998; Koenig & Knops, 2000; Kelly & Sork, 2002; Ascoli *et al.*, 2017; Vacchiano *et al.*, 2017; Fernandez-Martinez *et al.*, 2019). However, in moving forward, we also wish to emphasize our inability to account for most of the global variation in CVp, as reflected in the relatively low R^2 values of our global model (Table 1). Most ($c. 79\%$) variation in CVp remains unexplained, suggesting that the many drivers of global variation in CVp are as yet unidentified.

Numerous challenges must be overcome to better explain current patterns of seed production and to anticipate how those

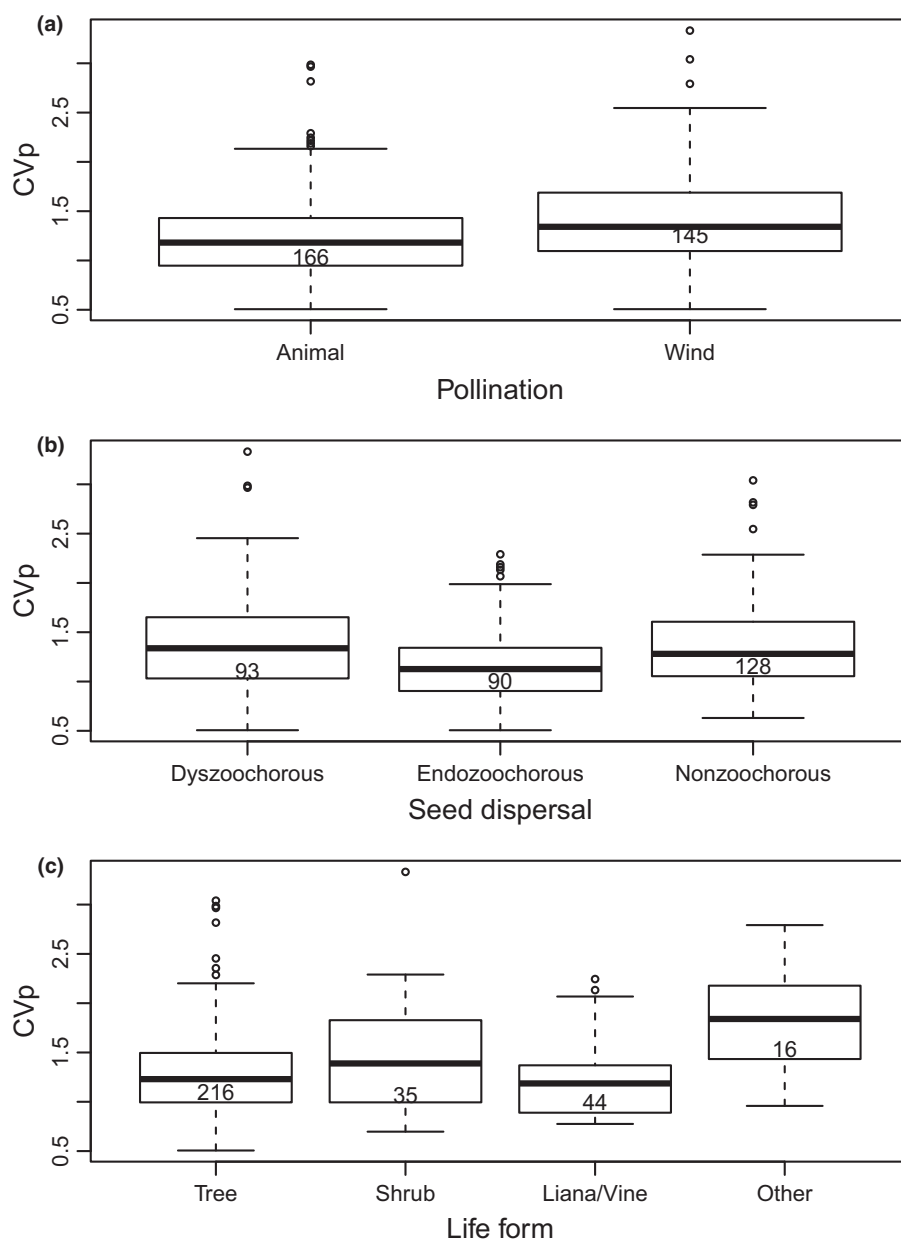


Fig. 5 Species-level variation in CVp due to plant functions of (a) pollination type, (b) seed dispersal type, and (c) growth form of plants. CVp varied by pollination type and dispersal type. The apparent increase of CVp in plants with 'Other' growth forms was largely driven by numerous datasets of *Chionochloa* bunch grasses. Numbers refer to sample size (number of species). Boxes show medians and 1st and 3rd quantiles, and whiskers are set at $1.5 \times$ interquartile range.

patterns might be affected in altered ecosystems and under changing climates (McKone *et al.*, 1998; Shepperd *et al.*, 2006; Tanentzap *et al.*, 2012; Pearse *et al.*, 2017). First, while the number and diversity of records of seed set have dramatically increased, there are still strong taxonomic and geographic biases to those datasets. For example, with the notable exception of *Chionochloa*, there are relatively few datasets of reproduction of long-lived grasses, despite the extreme species richness and ecological importance of perennial grasses. There are similarly few published long-term datasets of seed production in southeast Asia.

Second, we need to better understand why plants might evolve to have *low* CVp. There is substantial variation in CVp associated with geography, phylogeny, and life-history strategies of plants.

Research has focused on understanding the adaptive benefits of high CVp in terms of economies of scale. Aside from the inevitable demographic costs of delayed reproduction (Waller, 1979; Rees *et al.*, 2002), we know far less about the costs associated with high CVp. Considerable insight is likely to be achieved by the investigation of the selective costs and benefits to plant species that have low CVp, particularly across a range of environments where strongly masting species co-occur. Finally, we need to better understand the evolutionary processes driving CV of seed production. Two promising approaches to understanding the complex interplay of environmental variation and plant genetics as drivers of CVp are manipulative experiments (Bogdziewicz *et al.*, 2020) and the tools of quantitative and functional genetics.

Data availability

Data are available via ScienceBase at doi: 10.5066/P9U7278U.

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Author contributions

ISP conceived of the project and wrote the manuscript. ISP, JML, WDK, and ML compiled the dataset. ISP and ALH conducted comparative analyses. All authors edited the paper.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 A map of locations of seed set records.

Table S1 Model parameters during model reduction.

Table S2 Mantel tests of intraspecific spatial patterns in seed set variation.

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