

An assessment of temporal variability in mast seeding of North American Pinaceae

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Summary

Our overall objective is to synthesize mast-seeding data on North American Pinaceae to detect characteristic features of reproduction (i.e., development cycle length, serotiny, dispersal agents), and test for patterns in temporal variation based on weather variables. We use a large dataset (n=286 time series; mean length=18.9 years) on crop sizes in four conifer genera (*Abies*, *Picea*, *Pinus*, *Tsuga*) collected between 1960 and 2014. Temporal variability in mast seeding (CVp) for two-year genera (*Abies*, *Picea*, *Tsuga*) was higher than for *Pinus* (three-year) and serotinous species having lower CVp than non-serotinous species; there were no relationships of CVp with elevation or latitude. There was no difference in family-wide CVp across four tree regions of North America. Across all genera, July temperature differences between bud initiation and the prior year (ΔT) was more strongly associated with reproduction than absolute temperature. Both CVp and ΔT remained steady over time, while absolute temperature increased by 0.09°C per decade. Our use of the ΔT model included a modification for *Pinus*, which initiates cone primordia two years before seedfall, as opposed to one year. These findings have implications for how mast seeding patterns may change with future increases in temperature, and the adaptive benefits of mast seeding.

Introduction

Mast seeding is the spatially synchronous and highly temporally variable production of seed crops by a population of perennial plants [1–4], and is widespread both taxonomically and geographically [5,6]. In the most variable species, very large amounts of seed are produced infrequently, with few seeds produced in other years [7]. Strong temporal variation in seed-crop

production has important consequences for forest regeneration [8] and pulses of seed production have cascading effects in ecosystems [9,10]. For instance, mast seeding pulses in New Zealand lead to increases in non-native mammal populations that prey on native birds [10]; and obligate seed-eating birds in North America show widespread irruptions as a response to a lack of conifer seed during years of poor seed production [11]. Despite the critical role of mast seeding for an array of taxa, there is still a limited understanding of how mast seeding varies geographically and across species.

There are multiple hypotheses for the adaptive benefits of mast seeding (e.g., predator satiation and pollination efficiency) that suggest species with specific life history strategies will have greater temporal variability in seed crops [3]. High temporal variability is hypothesized to satiate seed-predators when seed production is high, enhancing pre-germination survivorship, and reduce seed-predator population numbers in the interval between resource pulses [12–14]. Conversely, species that are animal pollinated or animal dispersed are hypothesized to have lower temporal variability (measured as the coefficient of variation of the time series, CVp) to ensure sufficient populations of animal pollinators or dispersers [15,16]. Serotiny is a common life history strategy among fire-adapted conifers that also influences the adaptive benefits of mast seeding. Serotinous species retain their cones for years after seed maturation and their population persistence requires prompt regeneration after episodic, stand-replacing fire [17]. Because these species store their seeds aurally, with viable seeds as old as 20 years, there are fewer adaptive benefits of high CVp due to animal dispersal or to seed predation [18], and reproduction in serotinous species might vary due to resource matching [15].

It is generally agreed that the primary proximate cause of mast seeding is related to meteorological variables [19–23], especially temperature, and thus the temporal variability in seed crops may vary in relation to weather patterns in a given region. Specifically, for plants with two year reproductive cycles, seed crop size may not actually be driven by absolute summer temperature, but rather by the difference in temperature from the two previous

summers, referred to as the ΔT model [20]. In this model, the cue determining the number of initiated reproductive buds is the difference in temperature between the summer before the crop (year 't-1') and the temperature in the preceding summer (year 't-2'), with the resulting crop size (in year 't') a response to the sign and magnitude of the difference in those two earlier summer temperatures [20,24,25]. Simply, for those two-year reproductive cycle species that are cued by the temperature difference, a cool summer followed by a very warm summer induces a larger seed crop one year later [20,24,25]. The cues appears to be different for species in arid climates such as the US southwest, with cool and wet summers during bud initiation associated with large, subsequent seed crops in dryland forested ecosystems [26–28]; i.e. absolute temperature-regime matters [29]. Whether absolute temperature values or relative temperature compared to the previous year (ΔT) drive reproduction is critical to forecasting future mast events under a warming climate; if ΔT is the main driver then mast-seeding variability is not expected to change [20], whereas direct climate warming would lead to an increased cueing frequency that may induce a breakdown in mast seeding patterns over time [30]. While temperature appears to play a key role, the depletion of endogenous resources by a large reproductive event diminishes the number of reproductive buds the following year even when the conditions are favourable, such that high levels of reproduction do not happen in consecutive years [24,31].

Much of our knowledge on mast-seeding patterns comes from studies on one or a few species at relatively local scales. Compilations of mast-seeding databases have allowed for data across large areas and over long time periods to be used to answer questions about spatio-temporal dynamics [14,15,24,25,32,33], with massive global databases used to examine patterns broadly based on phylogenetic relationships and/or processes related to global change [5,6,34,35]. Global-scale studies have been useful in identifying broad patterns of mast seed production of plants, such as latitudinal gradients and associations with pollination and dispersal traits [6,15]. However, by combining information from such disparate plant taxa, these studies

struggle to understand the consequences of other plant traits. As a result, a more focused analysis of seed production among closely related species can help for understanding how plant life history strategies influence spatio-temporal patterns of mast seeding [6]. Here, we focus on North American conifers to identify broad patterns of seed production. In doing so, we limit our analyses to a geographic area and a phylogenetically-related collection of species to facilitate understanding of life-history strategies, including serotiny, types of seed dispersal, and the timing of seed development.

Pinaceae are common in North America across a range of habitats and environmental conditions, from hot and humid to cold and dry, and span a wide range of latitudes, and altitudes [36]. Pinaceae dominate the boreal forest and high altitudes, regions anticipated to be particularly vulnerable to climate change, as well as sandy, fire-prone terrain in the Southeast, and the coastal region of the Pacific Northwest. Conifer seeds are a key food resource for numerous species of animals, including birds, insects, and small mammals [37–39]. Most members of this family lack any capacity to asexually recruit from dormant basal buds following death of the crown, and thus we suspect that selection for higher or lower temporal variation in crop production will lead to stronger associations between traits and a measure of that variation. There are large numbers of long term datasets on conifer reproduction [5] as these species are key players in the forestry sector of the economy, and thus climate trends affecting temporal variability in crop production may be discerned.

Our overall objective is to synthesize mast-seeding data on North American Pinaceae to i) quantify relationships between CVp (the coefficient of variation of conifer reproduction data for the time series of a population) with life-history strategies and location, ii) to test for relationships between CVp between genera and tree regions; iii) assess changes in CVp over time across genera, and iv) examine the generality of the ΔT model relative to the absolute T model for Pinaceae in North America. We restrict the analysis to four genera with a large number of records (*Pinus*, *Tsuga*, *Picea*, and *Abies*), leading to a resulting data set of 286 time series

(mean = 18.9 years of data) spanning much of the continent of North America across 55 years (1960-2014). This dataset has a broader spatial distribution of sites, approximately 2,000 more years of data, and is an increase of nearly 50% in the number of continuous datasets since the last synthetic studies on mast-seeding in multiple genera of conifers [34,40].

Variation in CVp has been predicted to either increase at higher latitudes [15], or to peak and then decline at higher latitudes [6]. Elevation is also predicted to impact plant reproduction, with high elevation sites reducing reproductive potential and leading to lower CVp [22]. In addition to variability in CVp as a function of geographic location, we predict that CVp will vary among plants with different life history strategies, with animal-dispersed species and serotinous species predicted to have a lower CVp. We also compare CVp across four tree regions of North America (northern forests, Pacific coast, Rocky and western mountains, southeast coast [41]) and predict that more northern areas will have higher CVp. Given our data compilation extends back to 1960, we will also look for temporal trends in CVp. We also extend the ΔT model to temporal patterns of mast seeding for groups with contrasting seed developmental timing, and to groups within *Pinus* that occur in hot (low altitude, southern latitude) environments versus cool (high altitude /northern latitude) environments. For plant species with a 2-year cycle of development, reproductive bud primordia are initiated in year $t-1$, with the sequence of pollination through seed maturation completed in year t . By contrast, *Pinus* establishes the bud primordia in the summer of $t-2$, with pollination in $t-1$, and completion of seed maturation in year t . Thus, we reframe the ΔT model for *Pinus* with a suitable modification of the predictor variable (the temperature difference now based on $t-2$ minus $t-3$) to determine if this will lead to results consistent with two-year species. We tested the prediction that if the ΔT model holds, then rising temperatures over time will result in no change in ΔT , and subsequently there will be no change in mast-seeding variability [20] (except insofar as the slightly increased variation in local inter-annual temperatures is expected to increase slightly) [42–44].

Methods

Mast seeding data

Data on annual seed production were obtained from a mast-seeding database [5], augmented with data from searches of the literature and data repositories, and data from co-authors. All data included in analyses met the criteria that they i) had at least 6 years of mast seeding data for a species of coniferous tree in North America, ii) data were collected on a continuous scale (based on seed traps, visual cone counts, or cone scars), iii) occurred between 1960-2014. Additionally, iv) for a taxon to be included in the study, there was a minimum of 10 separate time series at the level of the genus. Data from distinct sites or on different species were included separately. Based on these requirements, we compiled a total of 286 mast seeding datasets with a mean time series length of 18.9 years and a total of 5,398 years of data, including four genera (*Abies* (n = 54), *Picea* (n = 87), *Pinus* (n = 126), and *Tsuga* (n = 19)) and 25 species (Fig 1; Table S1). This dataset includes a broader distribution of sites with data, approximately 2,000 more years of data, and is an increase of nearly 50% in the number of continuous datasets since the last synthetic studies on mast-seeding in multiple genera of conifers [34,40].

Data locations ranged across the continent and included four forest major regions of North America, northern forests, the Pacific coast region, Rocky and western mountain region, and the southeast coast region [41] (Fig 1). The 286 datasets cover 3,769 km in latitude and 3,456 m in elevation.

Life-history attributes

Attributes of each conifer species that are predicted to influence temporal variability in conifer reproduction were assigned to each species. These life-history attributes included: cone serotiny (no serotiny = 0; semi-serotiny or serotiny = 1), whether animals are recognized as a key dispersal agent for seeds (no = 0; yes = 1) based on having wingless or functionally wingless seeds [45], and the number of years required for seed-development, from bud primordia to seed maturity (2 years or 3 years) (Table S2). Attributes were assigned based on

the predominant status identified for a species. (e.g. our data set includes several records on the characteristically serotinous species *P. contorta*, however there may be some variability among populations. In a future paper we will show that non-serotinous and serotinous populations of both *P. contorta* and *P. clausa* have similar CVp values.

Climate data

We obtained climate data using ClimateNA v6.30, a software application that provides point-location climate data on a monthly, seasonal, and annual basis for a given year or time period over the entire continent of North America [46]. ClimateNA is based on the extraction and downscaling of gridded (4×4 km) monthly climate data for the reference normal period (1961–1990) based on PRISM [47] and WorldClim [48], and then using that as a baseline to downscale historical and future climate variables between 1901 and 2100. Climate data for specific point locations is accomplished through a combination of interpolation along with an elevation adjustment. We obtained monthly climate data for all mast seeding dataset locations between 1958 (two years prior to our first year of data) to 2014.

Analysis

Prior to analysis, we standardized each dataset to values between 0 and 100 based on the range of seed set values within each record because units of seed set varied among studies [5,24]. We calculated CVp for each dataset using annual values of reproduction across the duration of the data (standard deviation / overall mean). We built models to test hypotheses of whether CVp was driven by life-history characteristics or elements of geography (latitude, elevation). Life-history characteristics included serotiny of cones, animal dispersal of seeds, and seed-development time (as assigned above) at the species level (Table S2). We built linear mixed effects models with life-history characteristics, latitude and elevation and their interaction, and included random intercepts for site and mast-seeding data collection method (e.g., visual cone counts, seed traps, cone scars) to account for potential differences in the intercepts of CVp. The global model had five fixed effects and an interaction as described above, and we

191 compared all possible models of fixed effects and a null model using AICc model comparisons.
192 For each model, we weighted the contribution of each dataset by the number of years data were
193 collected for, as CVp can be influenced by the length of the time series. We ran this analysis for
194 all 286 conifer datasets combined and the best model(s) was determined using AICc model
195 selection and AICc weights to construct a 90% confidence-model set [49] and model-averaging
196 using the *MuMin* package [50]. All statistical analyses were conducted in RStudio using R
197 version 4.0.2.

198 We tested for variation in CVp across genera using a likelihood-ratio test between linear
199 mixed effects models with and without genera, with site and sampling method as random effects
200 using the *lmer* package [51]. We computed estimated marginal means for each group and did
201 post-hoc pairwise comparisons using the *emmeans* package [52]. We also tested for variation in
202 CVp across tree regions using a likelihood-ratio test between linear mixed effects models with
203 and without tree region, with site and sampling method as random effects and weights for the
204 number of years of data available for each dataset.

205 To test for changes in CVp over time, we split the 55-year span of the entire database
206 into three time intervals (1960-1977, 1978-1995, 1996-2014; interval length = 18 years, 18
207 years, 19 years; Fig. S1). We chose three time intervals because this approach provided an
208 interval length similar to the 20-year intervals used in [5]. For each time interval, we calculated
209 CVp for each dataset that had at least six years of data during that interval. We built a linear
210 mixed effects model with CVp during each time interval as the response variable, time interval,
211 genus, and their interaction as independent variables, and we included random intercepts for
212 site and mast seeding data collection method, as above. We also conducted this analysis
213 across tree regions with the same model setup (tree region replaced genus). We determined the
214 best model(s) from all possible models using the *MuMin* package [50] and AICc and AICc
215 weights for model comparison [49].

We tested for the influence of weather conditions and lags in reproduction on standardized reproduction. We reviewed conifer species profiles and found that July has been identified as a key month both across conifer species and across broad geographic locations within species [36]. Across North America, July has the hottest mean monthly temperature [53]. For genera with a two-year seed development time (*Abies*, *Picea*, and *Tsuga*), we used ΔT calculated from July temperatures in year t-1 minus July temperatures in year t-2 (ΔT_1), while for *Pinus* (three-year seed development, with cone primordia laid two years before seedfall) we modified ΔT to be based on July temperatures in year t-2 minus July temperatures in year t-3 (ΔT_2). We tested for general patterns in the influence of summer temperatures and lags in reproduction on annual reproduction for each genus separately, and for all two-year seed development time genera together. We built linear mixed effects models using standardized reproduction over the full datasets as the response variable. Models for genera with seed-development times of two years included each of July temperature in t-1 and ΔT_1 , both alone and with reproduction in the previous year (a 1-year lag in reproduction), the 1-year lag in reproduction alone, and a null model.

For *Pinus*, the genus with a seed-development time of three years, we first divided up the mast-seeding records for species based on their general climate conditions, with species located in 'hot' climates (*P. edulis*, *P. palustris*, *P. ponderosa subsp. scopulorum*, and *P. taeda*) analyzed separately from *Pinus* species located in 'cool' climates (see Table S1), identified based on [36]. This was done as we hypothesized that the relationship between temperature and reproduction may vary among hot and cool pines, with hot pines expected to be negatively associated with temperature [26,27]. The *Pinus* models included a term for reproduction two years prior (a 2-year lag in reproduction), July temperature in t-2 and both ΔT_2 and ΔT_1 . For all the above models, we included random intercepts for site, species, and year (for *Tsuga*, species was not included as a random effect because having only three species led to a singular fit), and weights based on the number of years in a dataset. For each level of analysis we

determined the best model(s) using the MuMin package [50] and AICc and AICc weights for model comparison [49]. We calculated variable importance values and model-averaged parameter estimates (and 95% confidence intervals) for standardized conifer reproduction patterns over time from the 90% AICc confidence model set for each of set of models run.

Lastly, we tested for temporal changes in July temperature and ΔT at each site for the duration of the study period. We built linear mixed effects models for each of mean July temperature and ΔT , with year, geographic region, and their interaction as response variables, and site as a random effect. We compared these full models to models based on subsets of these terms and a null model using AICC model comparisons.

Results

Across the 286 data sets, the interannual variability in seed production within a given population (CVp) had a mean of 1.57 (median CVp = 1.52). There was a wide distribution in CVp values, with a minimum of 0.54 and a maximum of 3.56 (Fig 2).

CVp – relationships with life-history attributes and location

Seed development time and serotiny were associated with CVp: the top model for CVp across all mast seeding data included the fixed effects of seed-development time and serotiny, which had an AICc weight of 0.723 (Table S3). The next best model included fixed effects of seed development time, serotiny, and animal dispersal ($\Delta AICc$ of 4.21, $w_i = 0.088$). Variable importance values for life-history attributes terms across all of the candidate models were 1.00 for seed-development time, 0.96 for serotiny, and 0.12 for animal dispersal. Importance values for location-based terms were 0.13 for elevation, 0.05 for latitude, and <0.01 for their interaction. The CVp of mast-seeding datasets with a three-year seed-development time were 0.37 lower than those with a two-year development time, and serotiny resulted in a lower CVp by 0.47 (Table 1). The 95% CI of model-averaged parameter estimates for animal dispersal, elevation,

and latitude all overlapped zero; there was no relationship between animal dispersal, elevation, or latitude on CVp.

CVp – relationships across genera and tree regions

There was a significant difference in mean CVp across conifer genera ($\chi^2 = 24.28$, $df = 3$, $P < 0.001$) with the mean CVp of *Pinus* spp. (1.26 ± 0.50) being significantly lower than both *Abies* spp. (1.93 ± 0.50 ; $t = 4.47$, $P < 0.001$) and *Picea* spp. (1.76 ± 0.52 ; $t = 5.24$, $P < 0.001$; Fig. 3). The mean CVp of *Pinus* spp. was not significantly different than *Tsuga* spp. (1.79 ± 0.44 ; $t = 2.24$, $P = 0.11$), and there were no significant differences in mean CVp between other genera. There were no significant differences in mean CVp across four tree regions of North America ($\chi^2 = 2.84$, $df = 3$, $P = 0.42$; Table 2).

CVp – changes over time

We found no evidence for a change in CVp over time at the genus level or across tree regions (Fig 4; Table S4), suggesting that there was no directional change in temporal variability in mast seeding between 1960 and 2014. AICc model comparisons, with time interval, genus, and their interactions as independent variables, showed that the null model was the top model (AICc weight = 0.810; Table S4). AICc model comparisons based on tree regions, with time interval and their interaction as independent variables also showed that the null model was the top model (AICc weight of 0.793; Table S4). There was no difference in these conclusions (no change over time detected) when the 55-year timeframe was separated into five time intervals of 11-years, compared to the three longer time intervals shown here.

Modelling mast-seeding dynamics - influence of temperature and lag-reproduction

Across all genera, ΔT variables were most strongly associated with standardized reproduction, suggesting that ΔT rather than absolute temperature most strongly drives reproduction. For *Abies*, *Picea*, and *Tsuga* reproduction was associated with ΔT_1 and reproduction the prior year ($\text{Reproduction}_{t-1}$): these two variables were in the most parsimonious model (AICc weight = 1.000 for *Abies*, 0.942 for *Picea*, and 0.715 for *Tsuga* (Table S5). For

Tsuga reproduction, the second best model only included ΔT_1 (AICc weight = 0.283) (Table S5). For all two-year development genera combined, the most parsimonious model was $\Delta T_1 + \text{Reproduction}_{t-1}$ (AICc weight = 1.000). Regarding the direction of effects of the independent variables on standardized reproduction, for all two-year genera (i.e. *Tsuga*, *Abies*, and *Picea*), ΔT_1 had a positive association with reproduction in year 't', while the lag in reproduction from the previous year ($\text{Reproduction}_{t-1}$) had a negative association (Table 3). For *Abies*, *Picea*, and the analysis of all two-year genera combined, the 95% confidence intervals of the parameter estimates did not overlap zero, which for *Tsuga*, the 95% CI for $\text{Reproduction}_{t-1}$ overlapped zero (Table 3).

For *Pinus*, the genus with a three-year seed-development time, reproduction of both cool and hot species was associated with ΔT_2 (the difference in July temperature during the year of cone initiation (two years prior to seed maturation) and the year prior); the importance value of ΔT_2 was 0.78 for cool species and 0.98 for hot species. Contrary to the patterns in the two-year development time genera, for both hot and cool *Pinus* species, increasing values of ΔT_2 had negative effects on standardized reproduction in year 't' (Table 3). In other words, a hot summer prior to cone initiation followed by a cool summer during the year of cone initiation leads to high reproduction of *Pinus* whereas the reverse is true for the other genera. For the hot group, multiple cooling years may be important (both ΔT_2 and ΔT_1 are in the top models; Table S5). For cool groups, the top models have both $\text{Reproduction}_{t-1}$ and ΔT_2 ; note that for the cool group all 95% confidence intervals overlapped zero (Table 3). For the hot group, only ΔT_2 did not overlap zero.

Mean July temperature and ΔT – changes over time

Mixed models indicated mean July temperature across study sites has increased over time (1960-2014). The top model (weight = 1.000) included only tree region and year as fixed effects, with no significant region*year interaction. Overall, temperatures increased by an estimated 0.5°C during the study, at a rate of $0.091 \pm 0.008^\circ\text{C}$ (mean $\pm$ SE) per decade. The

southeast region was warmest, with the northern tree region being the coolest, with the Pacific coast being similar to the northern region, while the Rocky and western mountain region had the widest range of temperatures (Fig. S2). For ΔT , model selection based on AICc indicated that the null model was the most parsimonious (weight = 0.974) suggesting no change in ΔT over time in any of the tree regions. The next best model included year and had a $\Delta AICc$ of 7.25 and a weight of 0.026 (Fig. S3).

Discussion

The North American conifer species analyzed here displayed nearly as much variability in CVp values (0.54 to 3.56) as analyses based on mast seeding datasets around the world [6]. Across four genera representing 25 species of conifers in North America and 286 datasets, temporal variability in mast seeding was related to seed-development periods, serotiny, and genus. All species of *Pinus* included in this study take three years for their seeds to develop, and had a lower CVp compared to the other genera with two-year seed-development periods; *Abies*, *Picea*, and *Tsuga*. In addition to highlighting differences in temporal variability in mast seeding among genera and life history strategies, our study documented widespread support for the ΔT model across genera as opposed to absolute temperature and found that both CVp and ΔT remained steady over the time period examined (1960-2014) while absolute temperatures increased. These findings have important implications for how mast seeding patterns may change with future projected increases in temperature and the adaptive benefits of mast seeding.

Serotinous species had lower temporal variability in mast seeding. Rather than selecting for high CVp to satiate seed predators, these serotinous species are instead more likely to have temporal patterns of reproduction that reflect resource matching [15], and selection for enhanced cone and seed defenses to reduce seed predation [54]. We had lower support for animal dispersal in driving CVp patterns across species, which differs from other studies that

found seed dispersal by animals was related to lower CVp [6,55]. Our classification of a species as animal dispersed was based on reports of successful dispersal and growth related to animals and if the wing was absent or so short to allow for wind dispersal [45]. Other studies have separated endozoochorous seed dispersal (seeds that are commonly passed through the gut of animals) and those seeds dispersed by animals that commonly consume cached seeds (dyszoochorous) [6].

We found no support that CVp varied geographically in relation to elevation and latitude. While CVp has been predicted to increase with latitude, both Kelly and Sork [15] and Pearse et al. [6] found a humped-shaped relationship that peaked at approximately 40° latitude and decreasing towards the poles, our data likely fit the declining portion of that trend. While *Pinus* had CVp values significantly lower than the other genera, there were no significant differences in CVp across regions. This suggests that mast seeding patterns of conifers in northern forests, which includes the boreal forest of Canada and Alaska, are no more or less variable on average than in forests in the south, which included data from Florida, USA.

We found that, as predicted by Kelly et al. [20] there have been no changes in CVp for North American conifers over the timeframe of 1960-2014. By contrast, Pearse et al. [5] used 20-year intervals from 1900-2014, and with a worldwide dataset found that CVp increased over time, for the whole dataset and with only Pinaceae. Partly this difference in conclusions might be traced to the longer time span available to them or their wider spatial coverage. We do point out however that extending their temporal record back twice as far as ours, entailed risks: e.g, there would be only 27 data points (5 authors; 5 species; different sites) in the first 40 years, and 14% of these data (far higher than for the rest of the record) were for a serotinous species, which, as demonstrated here, has a reduction in CVp of 0.47 compared to non-serotinous species. Thus, the documented increase in CVp may be a result of the limited data available that tended to favor a lower CVp in the early part of the record. In fitting models of standardized reproduction over time, we found that ΔT based on July temperatures was included in top

models, and that ΔT_1 was in the most parsimonious model for each of the two-year genera separately and for all of them combined. Similarly, for *Pinus* the three-year genera, ΔT_2 has importance values of 0.78 for the cool species and 0.98 for the hot species. With ΔT being a highly important variable, particularly when compared to the actual absolute July temperature one or two years prior to seed maturity, our finding of no change in CVp or ΔT over time is internally consistent. In addition to ΔT , a one-year lag in reproduction had high importance in reproduction models for *Abies*, *Picea*, and *Tsuga*, with a negative impact on conifer reproduction. In contrast, for *Pinus*, there was a slight positive effect of reproduction lags two years prior in cool species, and a very small negative effect of lagged reproduction in hot species. *Pinus* data showed lower variability across years compared to the other genera, suggesting perhaps that some individuals in those populations may be reproducing most years. The lag effect of reproduction would be expected to be stronger in those species with higher CVp.

For all of the two-year development time genera, warmer ΔT_1 values were related to greater levels of standardized reproduction. This finding is consistent with other research within these genera [24,56]. For *Pinus*, we created a modification of the ΔT model, because the cone primordia are differentiated two years before seedfall as opposed to the usual one year prior; while ΔT_2 had high importance in model selection; for both the cool and hot locations, higher ΔT_2 had a *negative* impact on the amount of standardized reproduction. In other words, cool years at the time of cone initiation that were preceded by hot years lead to high reproductive years, which is the opposite to what we observed with *Abies*, *Picea*, and *Tsuga*. For pine species adapted for hotter climates, we had hypothesized this negative relationship given these species are more likely to be water-limited rather than energy-limited and prior research has found negative relationships with hot temperatures during cone initiation and reproduction within this group of species [26–28]. Yet for the cooler pines we had hypothesized a positive relationship, similar to what we observed with all other genera. The observed negative relationship of these

cool *Pinus* species similar to the hot *Pinus* species, may be that the adaptive cue to signal reproduction was developed early into the evolution, as *Pinus* tended to occupy seasonally dry environments [57]. Abnormally hot July temperatures in the year prior to reproductive bud induction that lead to greater vapor pressure deficits [58] may thus increase water stress and therefore signal the tree to promote higher cone set for this more drought-adapted genus.

While the data used in our analyses included nearly 300 datasets and spanned vast distances, from Florida to Alaska (over 3,700 km of latitude) and 3,450 m of elevation, there are areas where mast-seeding coverage in conifers is sparse to non-existent, which is a limitation of this study (that being said, much of the interior United States and part of Canada are defined as prairie ecosystems without dense forests). Different methods of data collection and sampling regimes (e.g., number of samples, seed trap size, size of trees sampled) influence CVp values where too small seed traps will rarely catch seed, and small trees that rarely reproduce will both result in false zeros and elevated CVp values [59,60] and efforts could be made to standardize sampling. Future data collection should involve increasing the spatial spread of mast seeding data collection in both the United States and Canada, particularly for *Abies*, *Pinus*, and *Tsuga*. However, even for *Picea*, while the coverage may appear better, there are gaps in the data and some data are historic and are no longer being collected. Also, there are some species within the genera presented here that were not included due to lack of data, as well as some genera with only a few records that we could find. Note that there is confounding between the genus *Pinus* and three-year development times.

The goal of this study was to examine Pinaceae generally, there may be dramatic interspecific and intraspecific variation to be explored. For example, in a hot *Pinus* species, *P. edulis*, CVp is highest in more climatically stressful sites (high water deficits and low monsoonal precipitation) [61]. Thus while we detected no broad patterns in CVp across regions, more localized patterns may exist within species [24,62]. In addition, increasing data collection across elevational gradients at different latitudes in mountainous areas will allow for documenting mast

seedling patterns over time and testing hypotheses related to climate change. While temperature increases are predicted to be substantial at high latitudes, other components of climate change include frequency and severity of fires, insect attacks, and extreme weather events [63], and increasing CO₂ has been shown to experimentally impact conifer seed production [64] and could impact long-term mast seeding patterns.

We found that there were similar temperature and lag-reproduction drivers in genera with the same seed-development times. This suggests that there could be interspecific synchrony between species that overlap in their spatial distribution, leading to widespread mast years (or, alternatively, poor crops) across regions that would have a much greater effect on vertebrate seed predator abundances than would the seed production dynamics of a single species. Across all genera examined, we found much greater support for the ΔT model, rather than absolute temperature, driving reproduction. In addition, we found no evidence of change in ΔT for the study duration, despite increases in mean July temperature. This suggests that recent and projected increases in temperature will not result in subsequent increases in reproductive output among *Picea*, *Tsuga*, and *Abies*, or declines in reproductive output among *Pinus* (but see [27]). This is also consistent with our finding that variation in mast-seeding patterns (CVp) has not changed over time for the four genera included here, which has implications for the wide array of wildlife species whose population dynamics are linked to mast seeding patterns [10,37,65–67].

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630

Tables

Table 1: Model-averaged parameter estimates (and 95% confidence intervals) for CVp of North American conifer trees from the 90% confidence model set (see Table S3). The estimates represent the expected change in CVp when moving from one value of the life-history attribute to the next¹.

	Term	Estimate (95% CI)
Life-history attributes	Seed development time (2 or 3 years)	-0.37 (-0.53, -0.21)
	Serotiny (0 = no; 1 = yes)	-0.47 (-0.81, -0.13)
	Animal Dispersal (0 = no; 1 = yes)	-0.01 (-0.11, 0.09)
Location	Elevation (100m)	0.001 (-0.007, 0.010)
	Latitude ²	-0.0005 (-0.0053, 0.0043)

¹e.g., The CVp associated with a 3-year seed development time is estimated to be 0.37 lower than the CVp associated with a 2-year seed development time.

²Latitude scale is in decimal degrees

639 Table 2: Mast seeding variability (CVp) within four tree regions of North America (as defined by
640 [41] between 1960-2014. Number of datasets (n) and means $\pm$ standard deviation are shown.

Region	n	CVp
Northern forests	84	1.53 ± 0.54
Pacific coast	68	1.75 ± 0.45
Rocky and western mountain	112	1.44 ± 0.62
Southeast coast	22	1.86 ± 0.64

641

642

643 Table 3: Model importance values and model-averaged parameter estimates (and 95%
644 confidence intervals) for standardized conifer reproduction patterns over time from the 90%
645 AICc confidence model set for each of four genera. Models for genera with seed-development
646 times of two years included a 1-year lag in reproduction and July temperature and ΔT_1
647 (temperature in July of year t-1 minus July of year t-2). When there was only one top model,
648 there are no importance values for terms. For the seed-development time of three years, the
649 models included 1 and 2-year lags in reproduction and July temperature and both ΔT_1 and ΔT_2
650 (temperature in July of year t-2 minus July of year t-3).

Genus	Seed-development time	Term	Importance	Estimate (95% CI)
<i>Abies</i>	2 years	ΔT_1	na	2.18 (1.48 , 2.88)
		Reproduction _{t-1}	na	-0.17 (-0.22, -0.13)
<i>Picea</i>	2 years	ΔT_1	na	2.64 (2.03, 3.25)
		Reproduction _{t-1}	na	-0.10 (-0.15, -0.05)
<i>Tsuga</i>	2 years	ΔT_1	1.00	3.21 (2.23, 4.18)
		Reproduction _{t-1}	0.72	-0.09 (-0.21, 0.04)
<i>All 2-year genera</i>		ΔT_1	na	2.82 (2.47 , 3.17)
		Reproduction _{t-1}	na	-0.14 (-0.17, -0.11)
<i>Pinus (cool)</i>	3 years	Reproduction _{t-2}	0.99	0.17 (0.09, 0.25)
		ΔT_2	0.78	-1.49 (-3.32, 0.35)
		ΔT_1	0.32	0.10 (-0.63, 0.85)
		Temperature _{t-2}	0.21	-0.34 (-1.67, 0.99)
<i>Pinus (hot)</i>	3 years	ΔT_2	0.98	-2.72 (-4.22, -1.22)
		ΔT_1	0.50	-0.38 (-1.75, 0.99)
		Reproduction _{t-2}	0.14	-0.005 (-0.044, 0.034)

651

Figures

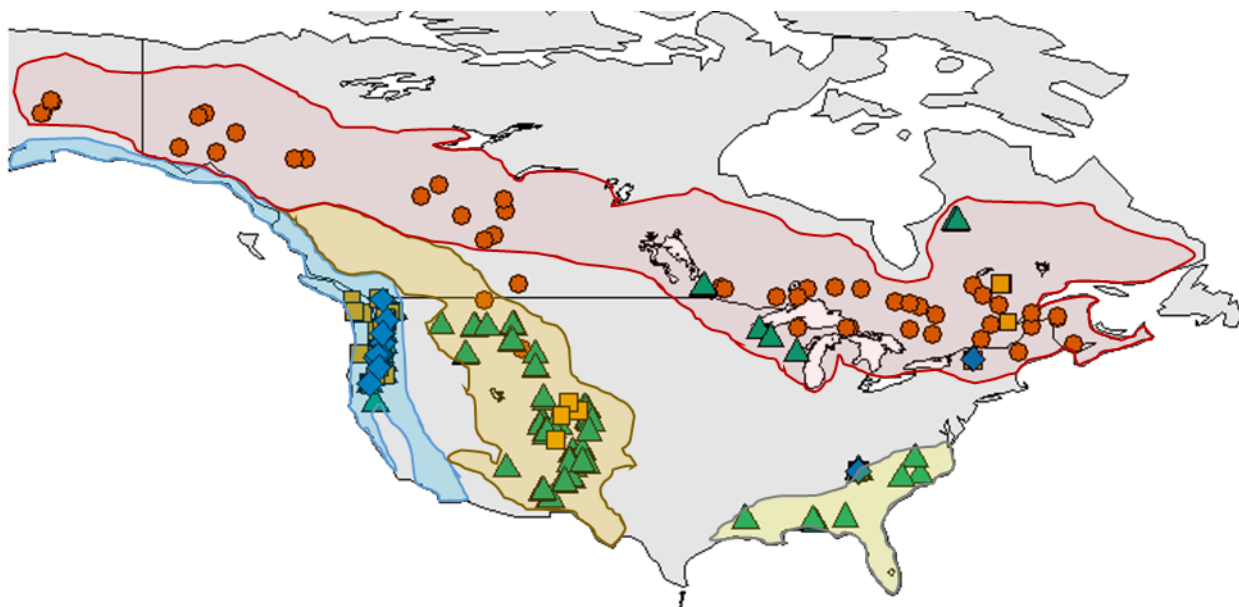


Fig. 1: Mast-seeding time series of North American conifers spanning 55 years (1960 – 2014). These data include 286 time series with a minimum of six years of data, four genera, a) *Abies* (orange squares; n = 55), b) *Picea* (vermillion circles; n = 87), c) *Pinus* (bluish-green triangles; n = 128), and d) *Tsuga* (blue diamonds; n = 20). Shaded areas represent the tree regions of northern forests (red), Pacific coast (blue), Rocky and western mountain (orange), southeast coast (yellow) (adapted from [41]). One *Picea* dataset in Medicine Hat, Alberta, Canada was included with northern forests for analysis, as it was a characteristically boreal forest species (*P. glauca*).

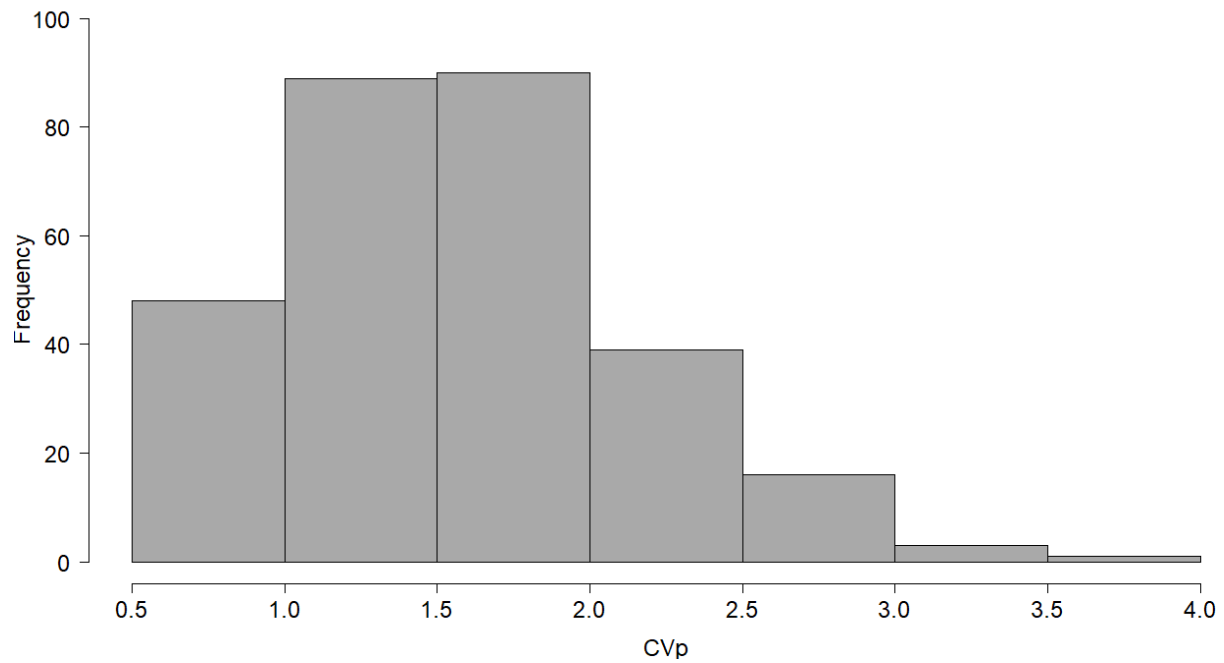


Fig 2. Distribution of CVp across mast seeding datasets by North American conifer tree species during 1960-2014 (n = 286 datasets).

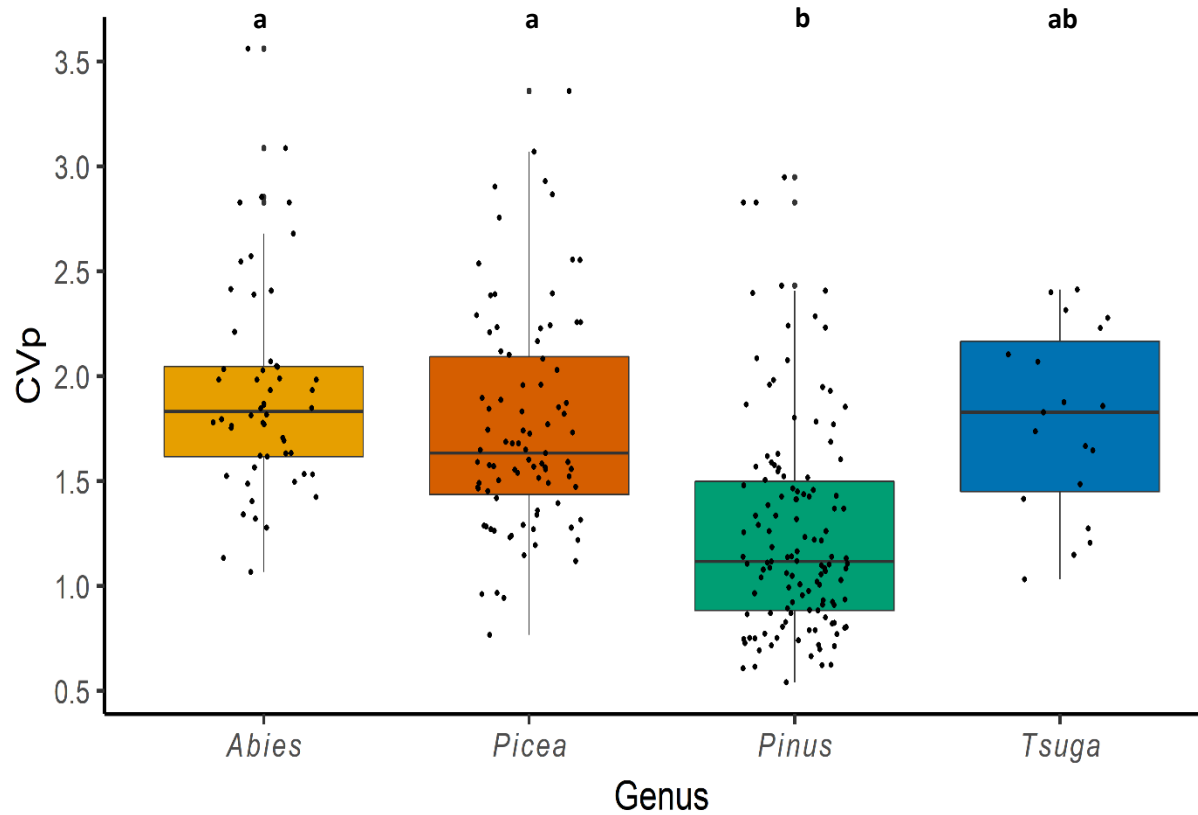


Fig. 3: Variability in mast-seeding patterns of North American conifers quantified as the coefficient of variation. These data include 286 time series with a minimum of six years of data, spanning 55 years (1960 – 2014). Letters indicate groups based on significant post-hoc tests for differences between group means; colours for genera match Fig. 1.

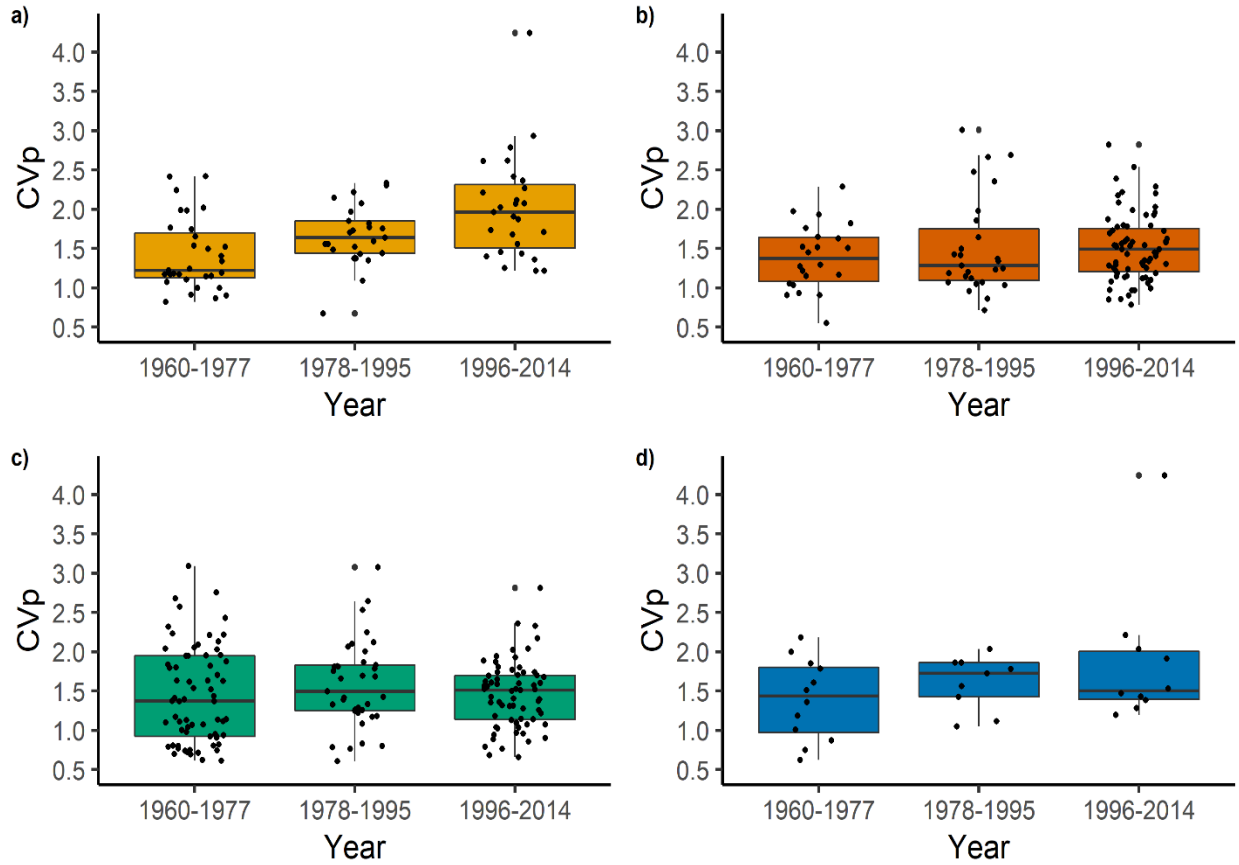


Fig. 4: Patterns of CVp over time for four genera, a) *Abies*, b) *Picea*, c) *Pinus*, and d) *Tsuga*. The entire time period (1960-2014) was split into three time intervals.