

Proximate drivers of population inter-annual variation in seed output for a masting conifer species

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ABSTRACT

Assessing the drivers of population inter-annual variation in reproductive output (CV_p) is key for conservation and management of forest resources, as these drivers determine variation in seed crops which are closely related to seedling recruitment (i.e. forest regeneration) and understanding the mechanisms by which they affect reproductive output sheds light into population-level resilience to changing abiotic conditions. Proximate drivers of CV_p include weather conditions which act as cues for reproduction and resource-driven lagged negative autocorrelations between past and current reproduction. Increased temporal variability in weather cues and strong negative autocorrelations are both expected to increase CV_p, but very few studies have robustly tested these predictions at the intra-specific level using long-term, multi-population datasets. Based on a published dataset, we used approximately 2,000 yearly observations spanning 130 years (1886–2015) and 61 populations to test for effects of temporal variability in weather cues and lagged autocorrelations on CV_p in seed output for a masting conifer species (*Picea abies*). We found that lagged (lag -1) summer (June–July) mean temperature was the best predictor of population-level annual seed output. Contrary to expectations, however, we observed a significant negative (not positive) effect of the standard deviation of lag -1 summer mean temperature on CV_p. In addition, we found a non-linear, hump-shaped relationship between lag -1 reproductive autocorrelation and CV_p, suggesting a qualitative change in the effects of resource constraints on reproductive variability whereby expected positive effects change to negative when the strength of negative autocorrelations exceeds a certain level. These patterns point at unexpected mechanisms whereby temporal variability in weather cues dampens variability in reproductive output, whereas the non-linear association with the lagged autocorrelations suggest thresholds associated with resource availability leading to qualitative changes in temporal patterns of reproduction.

1. Introduction

Individual plants in a population show high inter-annual variation in reproductive output (CV_i) and often reproduce synchronously leading to so-called masting events, i.e. large, highly synchronous seed output within a population (Kelly, 1994; Kelly and Sork, 2002; Pearse et al., 2016). Elevated CV_i and synchronous reproduction in turn result in high population-level inter-annual variation in reproduction (CV_p), another important feature of masting behaviour (Kelly and Sork, 2002). Following from observations of these marked and taxonomically widespread population-level dynamics in reproduction, a crucial challenge in masting research has been to understand the ecological and evolutionary forces that underlie CV_p in seed output, thus illuminating on the drivers of masting as well as its implications for plant and animal

communities and ecosystem function (Pearse et al., 2016). Identifying these drivers and the mechanisms by which they affect CV_p can also increase our understanding of closely linked temporal patterns in seedling regeneration and population-level responses to changing environmental conditions, key aspects for management and conservation of forests.

Much of the research on masting has focused on the proximate drivers of variability in reproductive output and synchrony (Bogdziewicz et al., 2020a). For example, weather variables have been shown to play a decisive role in dictating inter-annual variation in plant reproduction by acting as phenological cues. For example, the onset of reproduction and total seed output correlates with inter-annual variability in spring/summer temperature or summer precipitation (Pearse et al., 2014; Roland et al., 2014; Bogdziewicz et al., 2020b), differences

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in summer temperature between consecutive years (Kelly et al., 2013), or summer drought (Pérez-Ramos et al., 2010; Wion et al., 2020). To the extent that these cues modulate seed set across years (Koenig et al., 2015; Bogdziewicz et al., 2018), greater inter-annual variability in weather conditions would be expected to result in greater CV_p (hypothesis 1). A recent macroecological test reported on the effects of temporal variation in climatic cues on CV_p by testing the same cue across species (e.g. Pearse et al., 2020). However, species have been shown vary in the identity of weather cues affecting their reproductive output (e.g. Koenig et al., 2016; Moreira et al., 2019). This calls for studies addressing intra-specific variation in the association between weather cues and CV_p to elucidate variation in within-species climatic controls over CV_p which then informs interspecific comparisons.

Temporal variation in reproductive output can also emerge due to dynamics of resource use across years (Miyazaki, 2013; Crone and Rapp, 2014; Abe et al., 2016). Plants deplete significant amounts of resources (e.g. carbohydrates, mineral nutrients) during masting years (Smaill et al., 2011; Sala et al., 2012; Allen et al., 2017) which results in one or more subsequent years of low reproductive output, often resulting in negative correlations between past and current reproductive output, i.e. so-called lagged negative autocorrelations (Isagi et al., 1997; Moreira et al., 2015; Monks et al., 2016; Fernández-Martínez et al., 2019). Following from this, it is expected that increases in the strength of negative autocorrelations would result in greater CV_p (hypothesis 2). These plant endogenous processes could be associated to weather cues to the extent that abiotic conditions influence resource availability (Monks et al., 2016; Allen et al., 2017), such that studies jointly testing for these mechanisms are necessary to determine the independent effects of resource constraints and weather cues on CV_p .

In this study, we provide an intra-specific test of proximate drivers of CV_p in seed output for Norway spruce (*Picea abies*), a masting conifer species. Specifically, we asked: (1) Do weather cues consistently predict reproductive output across spruce populations and is interannual variability in such cues predictive of CV_p ? And (2) Are lagged negative autocorrelations between current and past seed output (potentially related to resource constraints) widespread across populations and are they predictive of CV_p ? Data from this study come from a published database including long-term measurements (>century) of annual fruit and seed set in *P. abies* and covering a large proportion of the species distribution in Europe (Ascoli et al., 2017a). Whereas previous work using this database tested how climatic variation affects long-term variation in *P. abies* masting across Europe by quantifying how much of the species distribution exhibited heavy seed crops each year (Ascoli et al., 2017b), here we describe CV_p patterns across populations and potential mechanisms behind them, one presumably operating via climatic cues and the other via resource constraints. Thus, by addressing two proximal mechanisms using a long-term, multi-population data set, the present work provides a detailed and robust assessment of within-species patterns of CV_p in reproduction and its potential drivers for one of the most widespread tree species in northern Europe. These findings can contribute to forest management and conservation by uncovering drivers of temporal variation in seed output and population responses to abiotic variation which determine seedling regeneration and population reproductive success under changing environments.

2. Material and methods

2.1. Natural history

Picea abies (Pinaceae) is a long-lived, evergreen tree native to most of Europe, and is distributed from northern Greece (39°N) to northern Norway (70°N). Its elevation range goes from sea level in Northern Europe up to above 2400 m. It is found mostly in areas with cool summer climates and rich sandy soils (Frankis, 1992). The species is also monoecious, producing separate male and female flowers (cone-like structures called strobili) in late spring. Female cones are green or

reddish, and mature 5–7 months after pollination (usually in September). Once they are dry, cones open and seeds are dispersed by wind. Masting events are common in this species (Gallego-Zamorano et al., 2018; Nussbaumer et al., 2018).

2.2. Literature search and data acquisition

We obtained the data for this paper from a published dataset (Ascoli et al., 2017a), for which the authors conducted a systematic review of the published data to reconstruct *P. abies* masting (Ascoli et al., 2017a). They searched peer-reviewed journals in ISI Web of Knowledge and Google Scholar, as well as non-peer-reviewed articles, unpublished data and books in Google Scholar, Google books, OPACplus of the Bavarian Central Library, the global Karlsruhe Virtual Catalog and the Austrian BFW literature database (Ascoli et al., 2017a). The search terms used were spruce masting in an appropriate selection of European languages (Ascoli et al., 2017a). Additionally, experts from governmental and private forest nurseries, ministries for the environment, and research institutes were contacted (Ascoli et al., 2017a).

Authors collected quantitative and qualitative data on fruit or seed set (Ascoli et al., 2017a). They recorded fruit and seed set in a variety of units and ordinal index (Ascoli et al., 2017a). Whereas previous work has conducted analyses using the full data set (e.g. Vacchiano et al., 2017), in the present study we used a subset of the full data set by restricting our analysis to series with a minimum of 6 years (Minimum = 6 years, Maximum = 65 years, Mean = 32.03 years) reporting continuous variables of seed or fruit production (e.g. counts per area, mass per area, volume per area, seed energy [calories] per area, percentage of fruiting trees). This yielded a total of 1,987 yearly observations from 61 populations distributed from northern Italy (45°N) to southern Norway (58°N) (Fig. 1), covering a time span from 1886 to 2015. Descriptive statistics of seed production in each *P. abies* population are shown in the Table S1 (Appendix A).

2.3. Statistical analyses

We calculated CV_p for each population as the standard deviation divided by the mean seed set across the time series. The CV_p did not continuously vary and was not unimodally distributed among seed set datasets (Fig. S1 in the Appendix A). Therefore, we log-transformed CV_p for all analyses described hereafter.

First, following Vacchiano et al. (2017) we tested for associations between reproductive output and several candidate climate variables to identify the best weather cue. Specifically, we performed Pearson correlations testing for an association between annual seed production and annual values for weather cues separately for each population. The following weather variables were chosen for these analyses based on a priori work with *P. abies* (Ascoli et al., 2017b), as well as other tree species (Vacchiano et al., 2017; Pearse et al., 2020): mean monthly temperature, monthly mean of daily maximum temperature, monthly mean of daily minimum temperature, total monthly precipitation, and potential evapotranspiration. We obtained annual weather time series of monthly climate data from the gridded database CRU TS 4.04 (0.5° resolution; years 1901–2019; <http://www.cru.uea.ac.uk/>). We calculated Pearson's r and associated P -values for each population and each weather variable across all 36 months of three-year period which included the calendar year of seed production and the two years prior to current seed production (i.e. lag -1 and lag -2) (Vacchiano et al., 2017). We considered significant correlation coefficients at the 95% confidence interval. We adjusted threshold P -value by a Bonferroni correction (0.05/36). In addition, following Vacchiano et al. (2017) we also ran correlations against aggregated summer (June–July) weather variables of one and two years before seed production. After identifying the best cue (i.e. that with the strongest and most frequently significant correlations across populations), we then ran linear and quadratic regression models with such cue as predictor of CV_p to decide whether to include

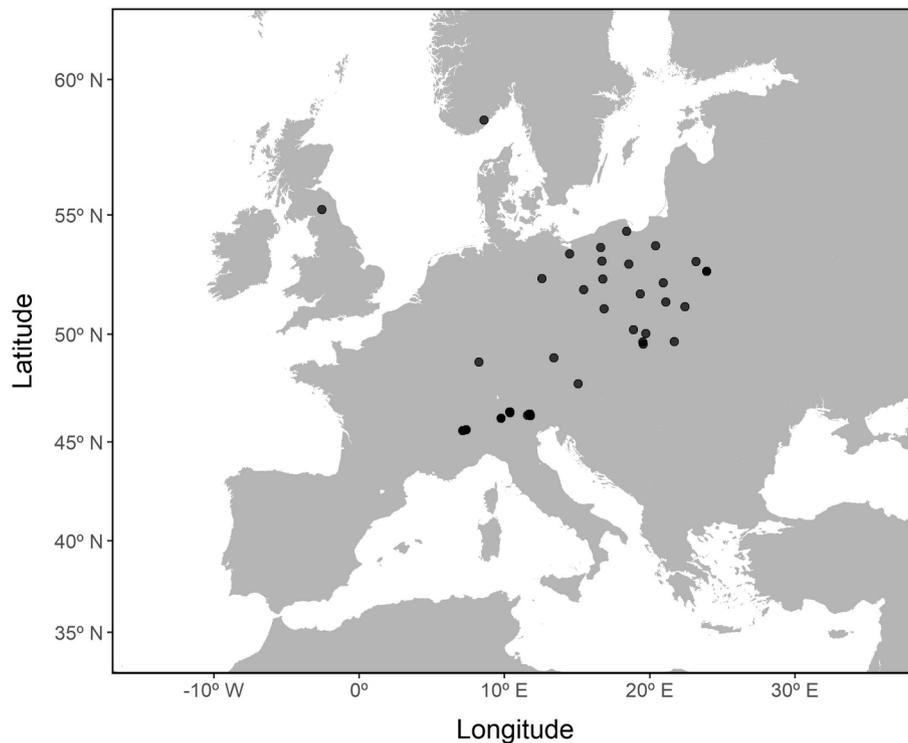


Fig. 1. Maps showing the location of all *Picea abies* sampled populations. The black dots indicate the populations.

only the linear or both the linear and quadratic terms for this predictor in the joint test for proximate drivers on CV_p (see ahead). We compared these models based on their Akaike Information Criterion (AIC) values; the model with the lowest AIC was taken as that with the best fit given the data (Burnham and Anderson, 2002). In addition, models for which the difference in AIC was <2 are taken to be equivalent (Burnham and Anderson, 2002).

Second, we estimated lagged autocorrelations between current and past seed output (lag -1) for time series of seed set using the *acf* function in the *stats* package of R (R Core Team, 2020). We then ran and compared linear and quadratic regressions with lagged autocorrelation as a predictor of CV_p . We compared these models based on their AIC values as above (Burnham and Anderson, 2002). In addition, to rule out a spurious association between lagged autocorrelations and CV_p as both variables were estimated from year-to-year variability in seed output, we performed a Monte Carlo procedure consisting of 10,000 multiple regressions independently generated upon randomized data (Morris et al., 2006). We obtained the distribution of F-values based on these simulations and calculated a *P*-value by comparing the observed F-value to this probability distribution.

Third, we tested for the independent effects of exogenous (i.e. weather) and endogenous (i.e. resource limitation) drivers of CV_p by running a population-level multiple regression jointly testing for the effects of the standard deviation (SD) of the weather cue and the lagged autocorrelation (fixed factors) on CV_p using the *lm* function in the *stats* package of R (R Core Team, 2020). We included linear or both linear and quadratic terms for each predictor based on the results from previously described linear and quadratic regressions run separately for each predictor.

Because CV_p can be influenced by the length of the time series (Pearse et al., 2017) we previously tested for an effect of this factor on CV_p and found it to be significant ($r = -0.37$, $P = 0.003$). Therefore, to control this methodological effect we ran weighted least squares models considering series length for all analyses described above. Finally, provided that recent work has reported on latitudinal variation in CV_p (Pearse et al., 2020) we also tested the effect of latitude on CV_p and

found that it was significant ($F_{1,59} = 40.18$, $P < 0.001$). Based on this, we included latitude as a covariate in all models described above.

3. Results

We found that lagged (lag -1) aggregated summer (June–July) mean temperature was the strongest and most consistent predictor of seed output (Fig. 2, Fig. S2–S5 in the Appendix A). Follow-up analyses indicated that a quadratic regression model with the standard deviation of this weather cue as predictor of CV_p , did not provide a better fit than the linear model ($AIC_{linear} = -5.89$, $AIC_{quadratic} = -3.98$; $\chi^2 = 0.09$, $P = 0.762$).

A quadratic regression with the lag -1 negative autocorrelation as predictor of CV_p , provided a better fit than the linear model ($AIC_{linear} = 13.80$, $AIC_{quadratic} = 10.55$; $\chi^2 = 5.25$, $P = 0.022$), and we therefore included both the linear and quadratic terms in testing for the lag autocorrelation in our joint analysis of CV_p drivers (see below). The Monte Carlo analysis indicated that the significant effect of the linear and quadratic terms of lag -1 autocorrelation on CV_p , was not spurious (linear term: observed F-value = 8.13, $df = 1, 57$, $P_{MonteCarlo} < 0.01$; quadratic term: observed F-value = 5.12, $df = 1, 57$, $P_{MonteCarlo} < 0.05$).

Based on the above, we ran a multiple regression model jointly testing for the effects of independent effects of each predictor, specifically the linear effects for summer temperature, and both linear and quadratic for the lag -1 autocorrelation. Results indicated a significant negative effect of the standard deviation of lag -1 aggregated summer (June–July) mean temperature on CV_p (Table 1, Fig. 3). In addition, we found a significant non-linear, hump-shaped relationship between lag -1 autocorrelation and CV_p (Table 1), whereby populations with moderately negative autocorrelations exhibited the highest variability in reproduction, whereas those at the extremes (i.e. highly negative or positive autocorrelations) exhibited the lowest CV_p (Fig. 4). We also ran follow-up models testing for each predictor separately and found that the joint model provided a significantly better fit than the former (Table S2 in the Appendix A), thus supporting the multiple regression as the optimal approach.

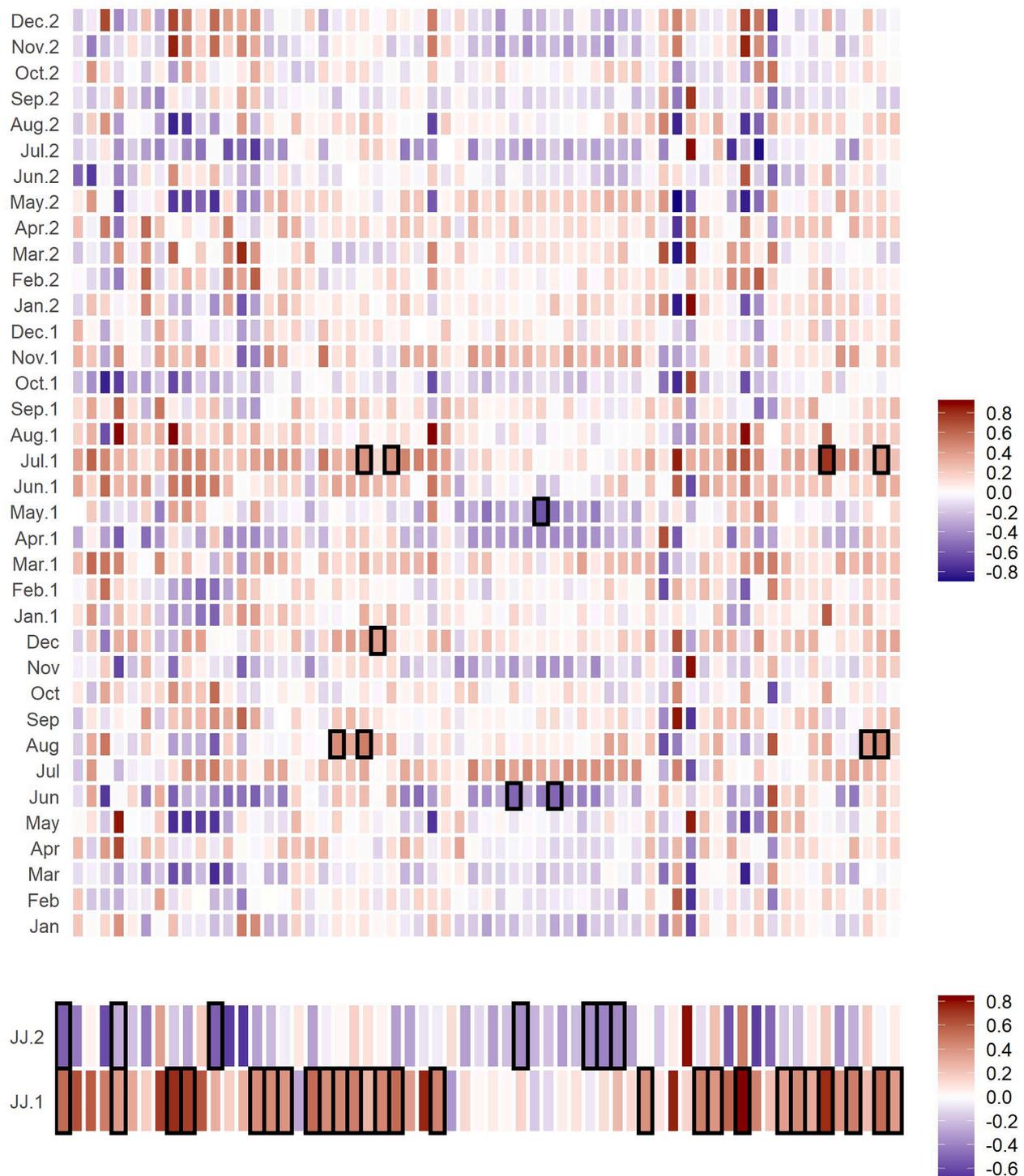


Fig. 2. Pearson correlations between monthly mean temperature and seed production for *Picea abies*. The larger portion of the figure shows correlations between mean monthly temperature for the present year, one, or two years before (e.g. Dec1 and Dec2, respectively) and seed production for each population (horizontal axis), whereas the lower portion shows correlations using either the mean summer (June-July) temperature one or two years before current output (JJ1, JJ2, respectively). Blue color indicates negative correlation coefficients whereas red color indicates positive correlation coefficients. Significant *P*-values are denoted by black squares (*P*-values for correlation coefficients for monthly climatic variables are Bonferroni-corrected, 0.05/36). For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

4. Discussion

Contrary to hypothesis 1, we found a significant negative (not positive) association between temporal variability in the weather cue (lag -1 summer mean temperature) and CV_p for *P. abies*. This finding mirrors the observed negative association between temperature variability and CV_p

reported across species by [Pearse et al. \(2020\)](#). However, contrary to this study which also reported a positive association between CV_p and variability in precipitation, in our case precipitation-related variables were not the best predictors of spruce reproductive output. The explanation may lie in that this species is distributed in humid temperate forests of central and northern Europe and is commonly found at mid to

Table 1

Results from multiple regression models testing for the effects of the standard deviation of lagged (lag -1) summer (June–July) mean temperature (SD mean temperature) and the linear and quadratic terms of the lagged (lag -1) autocorrelation on log-transformed inter-annual variation in seed output at the population level (CV_p) for *Picea abies*. The model also included the latitude as a predictor (see *Methods*). Slope estimates and their standard errors (SE), F-values, degrees of freedom of the numerator and denominator ($DF_{num,den}$), and significance levels (P) are shown. Significant ($P < 0.05$) effects are in bold.

	Estimate \pm SE	F-value	DF	P-value
SD mean temperature	-1.76 \pm 0.31	39.34	1, 56	<0.001
lag -1 autocorrelation	-0.61 \pm 0.18	4.04	1, 56	0.049
lag -1 ² autocorrelation	-1.69 \pm 0.53	9.99	1, 56	0.003
Latitude	-0.02 \pm 0.01	74.48	1, 56	<0.001

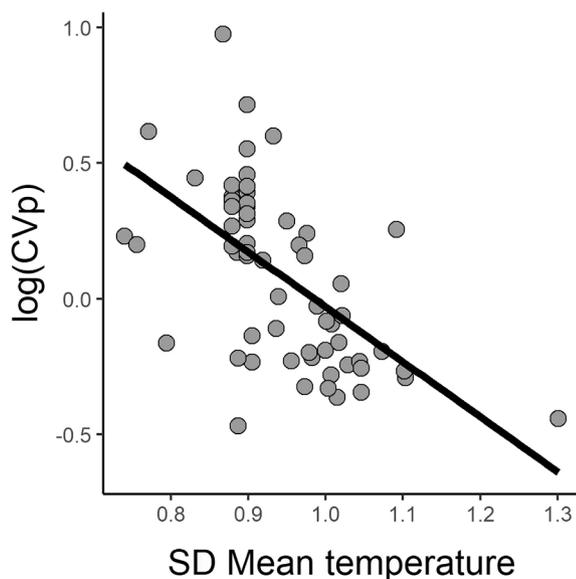


Fig. 3. Relationship between population-level standard deviation (SD) of lagged (lag -1) summer (June–July) mean temperature and log-transformed inter-annual variation in seed output at the population level ($\log CV_p$) in *Picea abies*. Grey circles represent tree populations ($N = 61$). The black solid line represents a significant ($P < 0.05$) relationship. Statistics from this model are shown in [Table 1](#).

high elevations, where reproduction may be more strongly influenced by temperature than precipitation. In contrast, species found in drier and warmer climates (e.g. Mediterranean-type) appear to be more responsive to precipitation variability (see [Pérez-Ramos et al., 2015](#); [Moreira et al., 2019](#)). It is important to point out that populations varied to a considerable extent in the strength of (positive) associations between temperature and seed output (see [Fig. 2](#)), a finding reported for at least one other species (*Quercus lobata*; [Koenig et al., 2020](#)). Such variation would presumably introduce noise in estimating the relationship between CV_p and SD temperature due to additional underlying population variability in temperature responses. However, in principle there is no reason to expect that this would contribute to generate the observed negative association between CV_p and SD temperature (e.g. that weakly sensitive populations have smaller CV_p and predominantly occur at sites with moderate to high temperature variability). While this suggests no apparent analytical or methodological aspects underlying the negative correlation between temperature variability and CV_p , further work is needed to understand the mechanisms by which weather variability contributes to long-term reductions in temporal variation in population reproduction in *P. abies* as well as other masting species.

Our results could be viewed as providing partial or inconsistent support for hypothesis 2 in that CV_p increased with increasingly

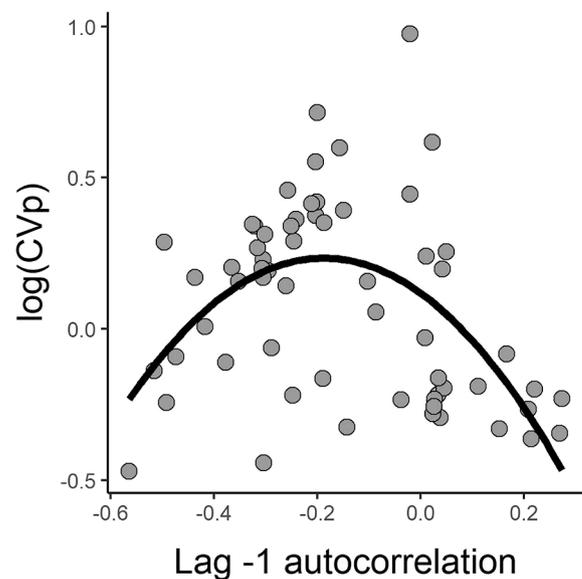


Fig. 4. Relationship between population-level lagged (lag -1) autocorrelations (estimated as the slope estimators from population-level regression between current and past seed output, see *Methods*) and log-transformed inter-annual variation in seed output at the population level ($\log CV_p$) in *Picea abies*. Grey circles represent tree populations ($N = 61$). Black solid line represents a significant ($P < 0.05$) relationship between $\log CV_p$ and lag -1 autocorrelations based on a quadratic model (see *Methods*). Statistics from this model are shown in [Table 1](#).

negative autocorrelations from weak (or absent) to moderately negative autocorrelations (as expected), but the relationship reversed from moderate to highly negative autocorrelations. This pattern mirrors the hump-shaped pattern reported by [Pearse et al. \(2020\)](#) across plant taxa. A reduction in CV_p under strongly negative lagged autocorrelations is difficult to explain if the latter are indicative of strong resource depletion as this would presumably result in fewer masting events of greater magnitude which would reduce the mean and increase the standard deviation across years (i.e. longer intervals between events as it takes longer to restore resources for the next large seed crop), thus increasing CV_p . Instead, the observed pattern suggests that CV_p is lower under strong resource constraints because masting events are of lesser magnitude and extremely infrequent which would disproportionately reduce the standard deviation (relative to the mean) across years. Correlations between CV_p and measurements of temporal variation in soil resources across populations (e.g. with naturally varying resource availability or along a resource gradient) and long-term manipulative experiments of resource availability are needed to test for bottom-up controls of resource availability and constraints on temporal variation in plant reproductive output.

Our joint analysis of endogenous (i.e. weather cues) and exogenous (i.e. resource availability) allowed us to test for the effects of each driver after controlling for the other on CV_p . In addition, the model with both predictors was more robust than either model testing for each one separately. Together, these findings indicate that the mechanisms behind these two effects exert independent effect on temporal variation in *P. abies* reproduction and that they better explain reproductive patterns in combination than separately. In addition, it is important to consider that these mechanisms may be contingent on each other. Our previous work with *Pinus ponderosa* and oaks ([Moreira et al., 2015](#); [Moreira et al., 2019](#)) showed that weather variables acting as cues for reproduction at the individual tree level also correlate with the strength of lagged negative autocorrelations, suggesting that responses to such weather cues could have evolved to minimize resource constraints and increase lifetime reproductive output. This could be scaled up to the population level (e.g. using super-producer trees as links to population-

level patterns; Minor and Kobe, 2017), namely that variability in weather cues relates to stand-level variability in resources and resource-based lagged autocorrelations, which in turn affect CV_p . Interestingly, we also observed dampening in the negative autocorrelation with increasing temperature variability ($r = 0.49$, $P < 0.001$), which could explain the negative correlation between temperature variability and CV_p (at weak to moderate autocorrelations, see above). Nonetheless, it is also important to consider that weather cues could directly influence negative autocorrelations independently of changes in resource availability (see Kelly et al., 2013). Therefore, the observed negative effect of weather variability on the CV_p might involve a direct influence and/or an effect occurring through changes in resource availability and the strength of the negative autocorrelation in reproduction. In this sense, the latter possibility would be more difficult to predict given non-linear effects of the autocorrelation on CV_p , and it is also possible that both mechanisms are operating at the same time further complicating predictions.

5. Concluding remarks

Recent studies (e.g. LaMontagne et al., 2020) including our own work (Moreira et al., 2015; 2019), emphasize the need for intra-specific assessments that jointly consider weather cues and lagged reproductive correlations to explain temporal (and spatial) patterns in reproductive output. To this end, long-term, more multi-population data sets of reproductive output (e.g. Koenig et al., 2016) are needed to robustly assess intra-specific patterns and elucidate species-specific proximal mechanisms. A better understanding of these mechanisms can inform forest conservation and management practices by considering the effects of population variation in seed output on seedling recruitment to assess population resilience to global change drivers such as climate change.

CRedit authorship contribution statement

Xoaquín Moreira: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Carla Vázquez-González:** Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization. **Luis Abdala-Roberts:** Conceptualization, Investigation, Methodology, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119562>.

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