



Mast seeding patterns are asynchronous at a continental scale

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Resource pulses are rare events with a short duration and high magnitude that drive the dynamics of both plant and animal populations and communities¹. Mast seeding is perhaps the most common type of resource pulse that occurs in terrestrial ecosystems², is characterized by the synchronous and highly variable production of seed crops by a population of perennial plants^{3,4}, is widespread both taxonomically and geographically⁵, and is often associated with nutrient scarcity⁶. The rare production of abundant seed crops (mast events) that are orders of magnitude greater than crops during low seed years leads to high reproductive success in seed consumers and has cascading impacts in ecosystems^{2,7}. Although it has been suggested that mast seeding is potentially synchronized at continental scales⁸, studies are largely constrained to local areas covering tens to hundreds of kilometres. Furthermore, summer temperature, which acts as a cue for mast seeding⁹, shows patterns at continental scales manifested as a juxtaposition of positive and negative anomalies that have been linked to irruptive movements of boreal seed-eating birds^{10,11}. Here, we show a breakdown in synchrony of mast seeding patterns across space, leading to asynchrony at the continental scale. In an analysis of synchrony for a transcontinental North America tree species spanning distances of greater than 5,200 km, we found that mast seeding patterns were significantly asynchronous at distances of greater than 2,000 km apart (all $P < 0.05$). Other studies have shown declines in synchrony across distance, but not asynchrony. Spatiotemporal variation in summer temperatures at the continental scale drives patterns of synchrony in mast seeding, and we anticipate that this affects the spatial dynamics of numerous seed-eating communities, from insects to small mammals to the large-scale migration patterns of boreal seed-eating birds.

The spatial scale of synchrony in mast seeding has important ecological implications¹² as it creates widespread pulses in the resources that are available to seed predators¹, and reduces pollination limitation in wind-pollinated species¹³. Increased reproduction in some species of oak leads to increases in the populations of mice and deer, increasing the incidence of Lyme disease². Mast seeding pulses in New Zealand lead to increases in non-native mammal populations that prey on native birds⁷, whereas obligate seed-eating birds in North America show substantial migrations in response to a lack of conifer seed during years of poor seed production^{10,14}. Although the spatial scale of synchrony is a key aspect of mast seeding ecology, few studies exceed the spatial scale at which synchrony in reproduction occurs^{12,15,16}. This is because mast seeding data are often collected on one or more species at a relatively local scale of one to tens of kilometres^{17,18}, but rarely at the regional or continental

scales unless species are lumped at the genus level to enhance the dataset^{8,19}. This creates challenges for evaluating hypotheses about spatial synchrony and the role of climate on mast seeding, in part because species within the same genus may have different developmental timing and life histories^{17,20,21}.

There are multiple hypotheses for the ultimate cause of mast seeding (for example, predator satiation and pollination efficiency³), and theory suggests that regionally correlated climatic variation (the Moran effect^{22,23}) is the main driver of synchronized seed production²⁴. Furthermore, it is generally agreed that the primary proximate cause of masting is weather related, because regional synchrony among conspecifics has no other probable explanation^{25–27}. For many plant species, summer temperature one or two years before the crop has a strong influence on the magnitude of seed production^{9,28–30}. The recently developed ΔT model argues that the difference in temperature from the two previous summers drives seed crop size³¹, and not absolute temperature. Additionally, the depletion of endogenous resources by a large previous crop diminishes the number of initiated reproductive buds the following year even in the case of favourable conditions^{32,33}.

Here we analyse spatial patterns in mast seeding of a transcontinental North American boreal forest species. We compiled mast seeding records in white spruce (*Picea glauca*), which is a predominant and widespread species of the boreal forest, during the period of 1985–2014. This resulted in 68 datasets at sites spanning distances of up to 5,227 km apart. We investigated three questions about the large-scale patterns of seed production in white spruce: (1) does synchrony in the reproduction of white spruce decay over large distances such that distant populations have juxtaposed and negatively correlated cone crops? (2) What spatiotemporal aspects of weather patterns drive the reproduction of white spruce across North America? (3) Can broad-scale patterns of weather anomalies explain synchrony and asynchrony in cone production across North America?

Mast seeding data showed high variability over time (Extended Data Fig. 1); the mean population-level coefficient of variation $CV_p \pm s.d.$ over all of the datasets was 1.65 ± 0.39 with a minimum CV_p of 0.81 (only 2 other datasets had $CV_p < 1$ (0.95 and 0.97)) and a maximum CV_p of 2.62. The highest synchrony in white-spruce reproduction was between sites at local scales (sites < 5 km apart), and significant synchrony persisted up to regional (around 1,000 km) scales (Fig. 1a). Spatial synchrony declined with distance, and was not significantly different from zero at sites that were 1,000–2,000 km apart. In contrast to previous studies, we found that synchrony in mast seeding patterns was significantly negative for sites that were greater than 2,000 km apart and this pattern of asynchrony extended to sites that were greater than 5,000 km

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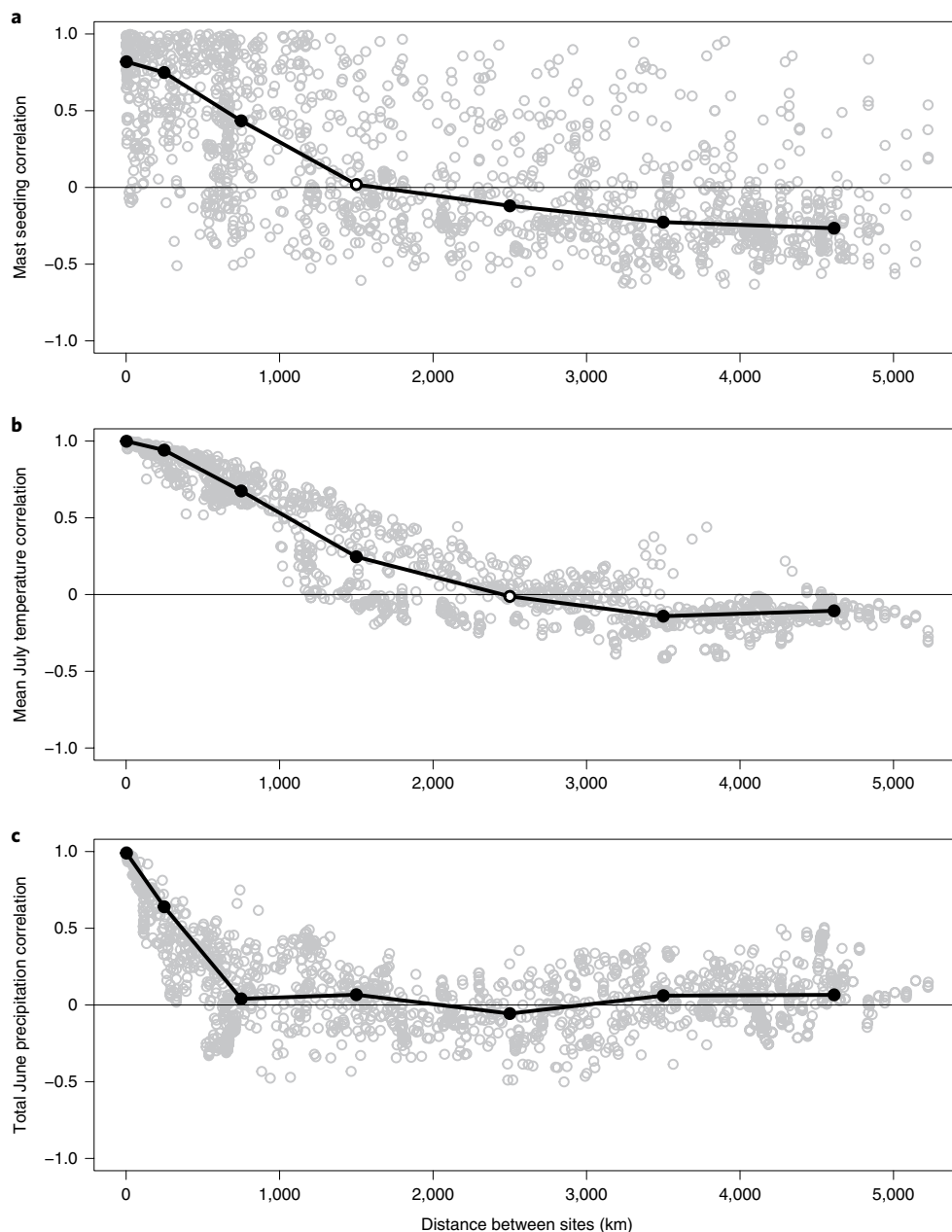


Fig. 1 | Correlograms for mast seeding and weather patterns between sites up to distances of 5,227 km apart. a–c. Spearman correlations are shown for white-spruce mast seeding (**a**), mean July temperature (**b**) and total June precipitation (**c**). Each grey symbol represents a pair of sites, with the median correlations for seven distance classes (<5 km, 5–499 km, 500–999 km, 1,000–1,999 km, 2,000–2,999 km, 3,000–3,999 km and 4,000–5,227 km) shown in black when significantly different from zero on the basis of bootstrapped 95% confidence limits, and white when not significantly different from zero.

apart. Corresponding declines in synchrony with distance were also observed in mean July temperatures (Fig. 1b), with negative relationships for distant sites, whereas synchrony in total June precipitation declined sharply across relatively short distances and was close to zero (although significantly different from zero) for all distances of greater than 500 km apart (Fig. 1c).

Variance in spatial synchrony of white-spruce reproduction was significantly explained by all of the models (all $P=0.001$; Extended Data Fig. 2). The model of mean July temperature (during year $t-1$) outperformed the model of proximity of sites alone, whereas the model of total June precipitation explained only 2.4% of the variance (on the basis of R^2). The saturated model did not explain much more of the variance than the mean July temperature of the

year before reproduction. In the saturated model, July temperature during year $t-2$ did not explain a significant proportion of the variance.

Part of the breakdown in patterns of spatial synchrony in mast seeding at the continental scale is reflected in the pattern of when and where resource pulses, or mast events, occurred. During 2005–2014, the pattern of mast events was variable both across and within regions, and often showed an east–west pattern of clustering (Fig. 2, Extended Data Fig. 3) that reflected patterns in summer temperatures (Fig. 3, Extended Data Fig. 4). The occurrence of mast events coincided with patterns of higher ΔT values (Fig. 3), such that regions with a large deviation towards warmer July temperatures compared with the previous year had mast events the

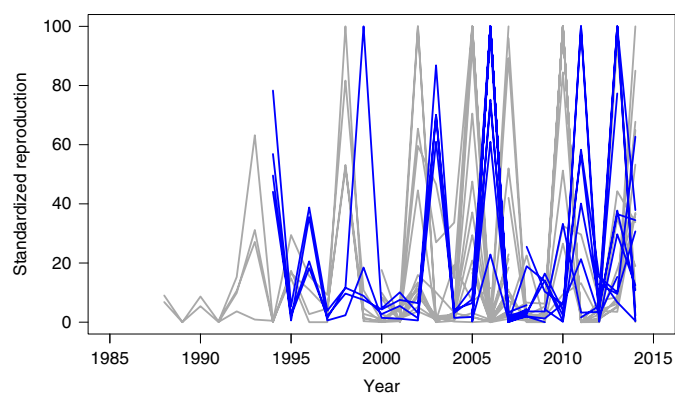


Fig. 2 | Mast seeding patterns for white spruce at sites in Yukon and Quebec. Patterns of east–west asynchrony are shown. The grey ($n = 20$) and blue ($n = 16$) lines represent mast seeding patterns for white spruce at sites in Yukon and Quebec, respectively. Plots of all of the sites in all of the regions are provided in Extended Data Fig. 1.

following year, and regions in which it was cooler compared with the previous year tended to not have mast events. The top model to characterize patterns in mast events (with an Akaike information criterion (AICc) weight = 0.97) had two terms, including a positive effect of ΔT with an odds ratio of 2.44 (95% confidence interval

(CI) = 1.82–3.27), and a negative effect of a mast event the previous year with an odds ratio of 0.17 (95% CI = 0.11–0.26; Extended Data Fig. 4). The next-best model also had two terms, including the long-term temperature anomaly and the previous-year mast event. The model of $2T$ and the previous-year mast event was the third best, and the ΔT model alone was the fourth best (Extended Data Fig. 4).

The relationship between ΔT for summer temperature and mast events at the continental scale is striking. For example, 2004 had relatively hot conditions in the west (Fig. 3a, 2004–2003) and, during the following year (2005), the only regions with mast events at any sites were in the west, in Alaska and Yukon (Fig. 3b, 2005). By contrast, during 2005, ΔT showed hot conditions in the east relative to the previous year (Fig. 3a, 2005–2004) and, during 2006, 83% and 93% of the sites within Ontario and Quebec had mast events, respectively, with no mast events in Alaska, Yukon or Alberta (Fig. 3b, 2006). Notably, July of both 2006 and 2007 was hotter than the previous year in western and central Canada (Fig. 3a, 2006–2005 and 2007–2006, respectively), but only 2007 had mast events at some sites in this region (Fig. 3b, 2007); by contrast, in 2008, no sites in this region had mast events (Fig. 3b, 2008), consistent with the impact of a mast event the previous year on the likelihood of a mast as shown in the model comparisons (Extended Data Fig. 4). 2010 was another year of mast events at sites in the west, with no mast events in the East (Fig. 3b, 2010). During this decade-long period (2005–2014), in all years except for 2009 (Fig. 3b, 2009), there were local mast events at some sites and often in multiple regions across the

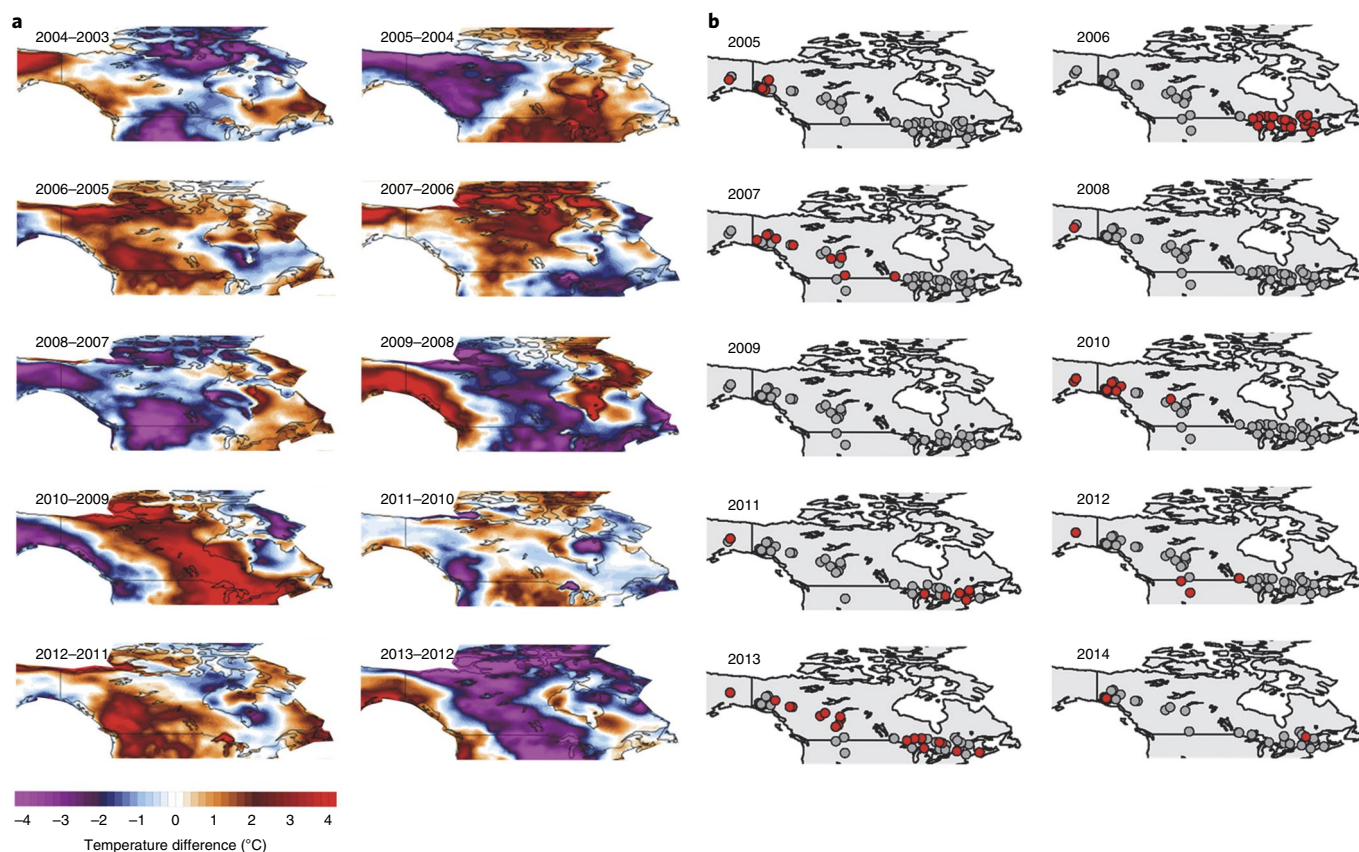


Fig. 3 | Maps of ΔT of mean July temperature and mast-event occurrence. **a**, Maps of ΔT of mean July temperatures (July temperature _{$t-1$} – July temperature _{$t-2$} ; data from http://cci-reanalyzer.org/reanalysis/monthly_maps/index.php) for the indicated time periods. **b**, Maps of mast events (red) and non-mast conditions (grey) at each white-spruce location during year t show the spatial patterns of temperature differences in earlier years and mast-year asynchrony during the period of 2005–2014. Maps in **a** positionally correspond to maps in **b**; for example, the ΔT of temperature in the top-left panel in **a** (2004–2003) corresponds to mast event occurrence the following year, shown in the top-left panel in **b** (2005). In cases for which there is no symbol representing a site in a panel, there were no data collected that year.

continent; 2009 followed a year (2008) that was mostly cool across North America relative to the previous year (Fig. 3a, 2008–2007). In 2012, ΔT showed warm conditions across most of the continent (Fig. 3a, 2012–2011) and, in 2013, there were some mast events at sites in regions all across the continent (Fig. 3b, 2013).

We demonstrated patterns of mast seeding synchrony for a dominant boreal-forest species, and uncovered asynchrony in mast seeding at large geographical scales ($>5,000$ km). Mast seeding was linked to summer temperatures and supports the hypothesis that reproductive pulses, or mast events, coincide with greater differences in summer temperature between the two years prior to seed production (the ΔT model³¹). We also found that a mast event during bud initiation significantly dampened the effect of a strong temperature difference. That is, a mast event is the result of both endogenous (resource depletion) and exogenous (weather) processes. Similar to other studies of spatial synchrony in mast seeding resource pulses, we saw a decline in synchrony with increased distance between sites^{8,34,35}.

Vacciano et al.³⁴ studied European beech across its distribution and found that, although synchrony declined with distance, it did not become negative. Koenig and Knops^{8,19} examined synchrony in mast seeding at a similar spatial extent to this study, with data pooled to genus where *Picea* included both species that mast seed (*P. glauca*, *P. engelmannii* and *P. rubens*) and a species with semi-serotinous cones and both lower mean cone production and lower variability in mast seeding (*P. mariana*); these pooled data showed declines in synchrony with distance, but not asynchrony. Uniquely, owing to the large spatial extent of our single-species dataset, we detected that, at distances between sites of 1,000–2,000 km, mast seeding was no longer synchronous, and that, at distances of 2,000–3,000 km or more, synchrony was significantly negative.

Weather conditions drive synchrony more than just the impact of distance alone and, therefore, the Moran effect²² seems to be key for mast seeding synchrony. Other studies have shown that components of the Northern Atlantic oscillation are correlated with continent-wide mast seeding patterns in European beech and Norway spruce (*Picea abies*) over distances of about 2,000 km (ref. 36). We used local precipitation and temperature data and examined their spatial patterns in North America over 5,000 km. Spatial synchrony in precipitation over 30 years was very high locally and declined rapidly, and correlations were close to zero at distances of greater than 500 km. As for temperature, we detected positive synchrony over about half of the breadth of North America and significant asynchrony over larger distances. Patterns of ΔT across the boreal forest contributed the best fit to explaining the occurrence of mast events. The temperature-anomaly model (mean July temperature the year before cone production minus the mean July temperature calculated between 1985 and 2 years before cone production, $\text{July temperature}_{t-1} - \text{mean July temperature}_{(1985 \text{ to } t-2)}$) did not perform as well as the ΔT model, because previous warm years included in the mean diminish the difference that is observed when comparing two consecutive years. Although numerous statistical correlations have been found between temperature and the production of seed cones, the exact mechanisms are unknown at present. The asynchrony at the continental scale represents an ecological dipole, which is similar to the pattern of east and west temperature dipoles that are observed in North America^{10,11}.

The range of white spruce is essentially that of the North American boreal forest, and its seeds are food for many species of small mammals, birds and insects³⁷. Mast seeding patterns impact animal populations locally, and synchronized patterns of mast seeding among individual trees have been shown to be highest at very local scales that coincide with the size of the territories of seed predators¹⁸. This research greatly extends the scope of studies in mast seeding synchrony to the continental scale. Although some species of seed consumers are impacted locally by synchrony

and pulses in seed production, there are other species that operate at much larger scales over regions or the continent. For example, boreal-forest songbirds have shown large east–west irruptive movements in North America that are correlated with climatic dipoles that are believed to be linked to mast seeding patterns¹⁰. Our research here shows evidence of asynchrony in mast seeding and high-reproduction mast events entrained by weather patterns at regional to continental scales.

Methods

Data sources. We compiled records of annual reproduction by white spruce from published literature, long-term records available online, and data provided directly by other researchers and co-authors. Sixty-eight datasets fitted the criteria that they (1) were direct quantitative records of white-spruce reproduction (that is, cone or seed counts), (2) included ≥ 6 years of data (because white spruce mast at intervals of 2–6 years (ref. 38) and (3) fell during the years 1985–2014. The dataset included a total of 836 site-years (mean length = 12.3 years, maximum length = 28 years) and spanned locations from Alaska, USA in northwestern North America and southeast to sites in New Brunswick, in eastern Canada. We standardized each dataset, using its long-term mean, to values of annual reproduction ranging from 0 to 100 before conducting data analyses^{5,19}. The proximity between sites was based on latitude and longitude given their Haversine distance (accounting for the curvature of the planet) using the geosphere package in R³⁹.

Weather data. Bud differentiation in white spruce occurs in July across much of its range; hot conditions at this time (year $t-1$) are a rough indicator of a large cone crop the following year (t)³⁸. Pollination occurs in June (of year t) and heavy rains can reduce seed crops³⁸. The best predictors of weather effects on reproduction for this species are mean July temperature and total June precipitation⁹, and these were obtained for each site at which we had reproductive data from the Daymet daily surface weather and climatological summary dataset (<https://daymet.ornl.gov/>)⁴⁰. Daymet provides daily modelled weather estimates at a spatial resolution of 1 km² on the basis of networks of thousands of weather stations from the National Oceanic and Atmospheric Administration, National Centers for Environmental Information and Environment and Natural Resources, Government of Canada.

Statistical analyses. As an overall measure of the temporal variability of mast seeding, we calculated the coefficient of variation ($CV = \text{s.d.}/\text{mean}$) for each dataset¹. Synchrony in mast seeding patterns was calculated using Spearman correlations between pairs of sites that had a minimum of six years of data overlap ($n = 1,587$ pairs). Spatial synchrony in each of mean July temperature and total June precipitation were determined using Pearson correlations calculated between pairs of sites that shared at least six years of mast seeding data between 1985–2014.

We used a spatial correlogram to examine patterns of synchrony in white-spruce reproduction across distances of up to 5,227 km (ref. 41). Distances between site locations were binned into 7 distance classes as follows: <5 km, 5 km to <500 km, 500 km to $<1,000$ km, 1,000 km to $<2,000$ km, 2,000 km to $<3,000$ km, 3,000 km to $<4,000$ km and $>4,000$ km. The median correlation coefficient for each distance class was compared to zero by creating 95% CIs using the percentile method from the boot package in R to determine significance⁴². Spatial correlograms across the same range of distances were also created for each of mean July temperature and total June precipitation across years.

To determine the relative importance of multiple factors on spatial synchrony in white-spruce cone production, we conducted multiple regression on distance matrices using the MRM function in the ecodist R library^{43,44}. These models included distance matrices representing (1) space (proximity between sites = $1 - (\text{distance}/\text{maximum distance})$ (refs. 44,45); (2) weather (mean July temperature in each of years $t-1$ and $t-2$, mean precipitation in June of year t); and (3) a saturated model with all parameters. The coefficient of the effect size and P value, along with model R^2 and the P value for each of the overall models were based on 1,000 permutations of the data.

To examine spatial patterns in the occurrence of high reproduction mast years or mast events, we classified mast events and non-mast events using the standardized deviate method⁴⁶. Generalized linear mixed-effects models were then used to test the relationship between temperature and the occurrence of mast events during 2005–2014; mast events were included as a binary variable. We created and compared four temperature-based models, including mean July temperature in the previous year (year $t-1$), mean July temperatures in years $t-1$ and $t-2$ (2T model³¹), the difference in mean July temperatures in years $t-1$ and $t-2$ (ΔT model³¹) and a temperature-anomaly model that included the difference in July temperature in the year $t-1$ compared with the long-term temperature at the site calculated as the mean July temperature between $t-2$ and 1985. We also included models with mast-year status in year $t-1$ to account for the finding that mast events do not occur in consecutive years⁴⁶. Random effects were included, with site as a random intercept in all of the models, and regions were included as random slopes for models that included temperature variables (temperature _{$t-1$} , ΔT , temperature anomaly and 2T). Following Dormann et al.⁴⁷, we tested for

spatial autocorrelation in the residuals after model fitting (using the *ncf* package⁴⁸ in R); we found no such patterns. Relative model fits were compared using AICc model weights, and overall model fits were assessed using the conditional R^2 for generalized linear mixed-effects models⁴⁹. The random effects are reflected in the number of parameter estimates (k) in AICc model fits; one parameter was added to estimate the variance that is related to the random site intercept, and three parameters (estimating variances and covariance) were added for models with one temperature variable in which random slopes for regions were used (that is, temperature _{$t-1$} , ΔT and temperature anomaly); the 2T model has a total of six parameters representing random slopes because it includes both temperature _{$t-1$} and temperature _{$t-2$} as variables. Models were run using the *lme4* package⁵⁰ and *MuMIn* package⁵¹ in R v.3.5.1.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.xsj3tx9bb>.

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Author contributions

Data were compiled by J.M.L., I.S.P. and W.D.K., and data were contributed by D.F.G. J.M.L. conducted the data analysis and wrote the manuscript with contributions from all of the authors.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41477-020-0647-x>.

Supplementary information is available for this paper at <https://doi.org/10.1038/s41477-020-0647-x>.

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Region	n	Years	$\bar{X}_{CVp}$	CV _p range
		(interval)		(min-max)
AK	9	1985 – 2013	1.92	1.15 - 2.55
YT	20	1988 – 2014	1.64	1.04 - 2.32
AB	10	1995 – 2014	1.74	0.81 - 2.62
ON	13	2005 - 2014	1.47	1.10 - 2.02
QC	16	1994 - 2014	1.50	1.00 - 1.94

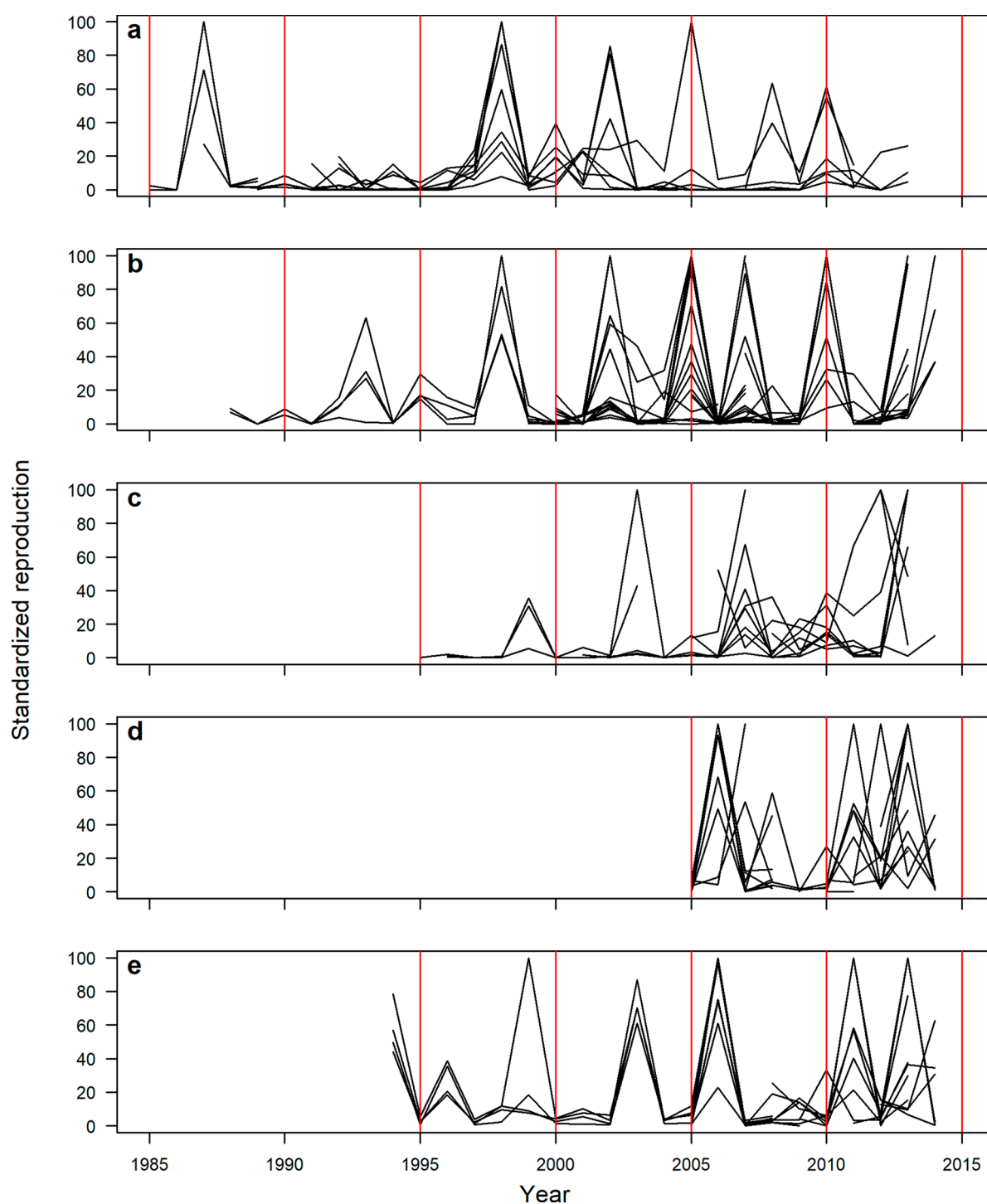
Regions are named by the province or state where the majority of datasets were located; AK – Alaska, YT – Yukon, AB – Alberta (including one site in each of Montana and Wyoming), ON – Ontario and includes one site in each of Manitoba and Michigan), and QC - Quebec (includes two sites in adjacent areas in New Brunswick and one site in Maine).

Extended Data Fig. 1 | Summary of 68 datasets on white spruce reproduction including the number of sites in each region (n).

Models and Variables	Coefficient	P (variable)	R ² (model)	P (model)
1.Space			0.095	0.001
Proximity	0.309	0.001		
2a. Weather			0.176	0.001
July temp t-1	0.419	0.001		
2b. Weather			0.174	0.001
July temp t-2	0.417	0.001		
2c. Weather			0.024	0.001
June precip t	0.154	0.001		
3. Saturated model			0.177	0.001
Proximity	0.044	0.001		
July temp t-1	0.424	0.001		
July temp t-2	-0.040	0.239		
June precip t	0.017	0.005		

‘July temp’ represents mean daily July temperatures in year t-1 and t-2, and ‘June precip’ is total June precipitation in year t.

Extended Data Fig. 2 | Multiple regression on distance matrices (MRM) results for spatial proximity and weather factors affecting mean synchrony of white spruce reproduction in year t.



Extended Data Fig. 3 | Time series (1985–2014) of standardized annual white spruce reproduction with a minimum of six years of data. Black lines represent individual time series from sites in five regions including: Alaska **a**, Yukon **b**, Alberta **c**, Ontario **d**, and Quebec **e**.

Model	k	Log-likelihood	ΔAICc	w_i	cR^2
$\Delta T + \text{MastYear}_{t-1}$	7	-157.8	0.00	0.970	0.55
Temperature Anomaly + MastYear_{t-1}	7	-161.5	7.38	0.024	0.55
$2T + \text{MastYear}_{t-1}$	11	-159.5	11.64	0.003	0.56
ΔT	6	-164.7	11.65	0.003	0.43
$2T$	10	-166.6	23.68	0.000	0.46
Temperature Anomaly	6	-180.1	42.35	0.000	0.34
$\text{MastYear}_{t-1} + \text{Temperature}_{t-1}$	7	-202.1	88.43	0.000	0.40
MastYear_{t-1}	3	-207.5	91.03	0.000	0.31
Null	2	-222.9	119.82	0.000	0.00
Temperature_{t-1}	6	-218.8	119.83	0.000	0.10

Extended Data Fig. 4 | Model comparisons for the occurrence of mast years in white spruce. Mast years are included as a binary response variable in generalized linear mixed effects models with temperature patterns and lag of mast years. 'k' represents the number of parameters in the model (see methods), ' ΔAICc ' is the sample-size corrected AIC value compared to the best model, ' w_i ' is the weight, and cR^2 is the conditional R^2 for each model based on both fixed and random effects.

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| ☐ | ☒ Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated |

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

- | | |
|-----------------|----------------------|
| Data collection | no software was used |
| Data analysis | R version 3.5.1 |

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Ecological, evolutionary & environmental sciences study design

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Study description	This study examines scales of synchrony in white spruce reproduction based on data collected from 68 locations in North America spanning over 5,200 km and the years of 1985-2014. Climate drivers of reproduction and synchrony of mast seeding events are tested.
Research sample	Data on white spruce reproduction were compiled from existing datasets, these included published data and unpublished data contributed by researchers. All datasets used in the study represented a minimum of 6 years of data collected annually at the same site.
Sampling strategy	Data were compiled from 68 sites based on available data.
Data collection	We compiled records from published literature, long-term records available online, and data provided directly by other researchers and coauthors
Timing and spatial scale	Data span 1985-2014, with annual data collection, and a minimum of six years of data. Sites spanned 5,227 km.
Data exclusions	All data shown in the study fit the inclusion criteria of having a minimum of six years of data collected at a site.
Reproducibility	None
Randomization	N/A - There were no treatments applied for this study.
Blinding	None
Did the study involve field work?	☐ Yes ☒ No

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Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
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☒	☐ Animals and other organisms
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Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging