See(d)ing the seeds - toward weather-based forecasting of annual seed production in six European forest tree species

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Abstract

1. Ecological forecasting is essential for addressing climate change adaptation and mitigation. In reforestation and habitat restoration, seed production forecasting will support planning and resource allocation, providing benefits for wildlife management and public health.

2. We hind- and forecast seed production using statistical models based on weekly weather and high-resolution seed data of six European tree species recorded in two Austrian old-growth forest sites. Using a sliding-window approach and model selection, we model annual reproduction for three coniferous (Silver fir, European larch, Norway spruce) and three broadleaved species (Sycamore maple, European beech, European ash). We investigate the change of explained variance with decreasing time before seed rain and evaluate hindcasting proficiency as well as the potential forecast horizon based on quantitative and categorical measures useful to stakeholders in the tree seed sector.

3. Most models show unbiased but partly imprecise predictions with a broad range in explained variance (0.15 to 0.93) in the year prior to seed rain. Nevertheless, within this timeframe, hindcasting seed rain above 10% of the long-term maximum, a threshold relevant to practitioners, works well for all species. Previous seed rain explains a large proportion of the variation in seed rain of fir, ash, and maple.

4. We forecast seed rain for 2022 to 2025 for all six species. Regarding categorical one-year-out predictions, results for 2022 and 2023 were mostly correct for beech, maple and larch, mixed for spruce and fir, and incorrect for ash.

5. *Synthesis and Applications:* Seed production is predictable with a promising degree of accuracy for most studied species one year in advance. This holds value for seed harvesters, nurseries, forest and wildlife managers, and may also inform seed orchard management and public health risk anticipation. Seed forecasts will help address seed scarcity and thus support climate change adaptation and mitigation. Future efforts should prioritise species based on seed storability and support the harvesting of rare species. Understanding reproductive strategies and their responses to climate change points the way forward. Further collaboration with user groups and implementing multi-level seed monitoring schemes will allow for tailoring further seed forecasts that transform the field.

Key Words: ecological forecasting; masting; seed production; forest restoration; mast seeding; forest reproductive material; tree seeds;

Introduction

Ecological forecasting has the potential to become a critical tool in supporting climate change adaptation and mitigation (Dietze *et al.* 2024), for example in reforestation and habitat restoration where uncertainty about annual seed production of target species results in logistical challenges or even project failures (Whittet *et al.* 2016, Jalonen *et al.* 2018, Pearse *et al.* 2021). Such projects often require large amounts of seeds within a short time frame, which can pose a challenge since reproduction by many perennial plant species is strongly variable in time with high spatial synchrony (see Fig. 1).

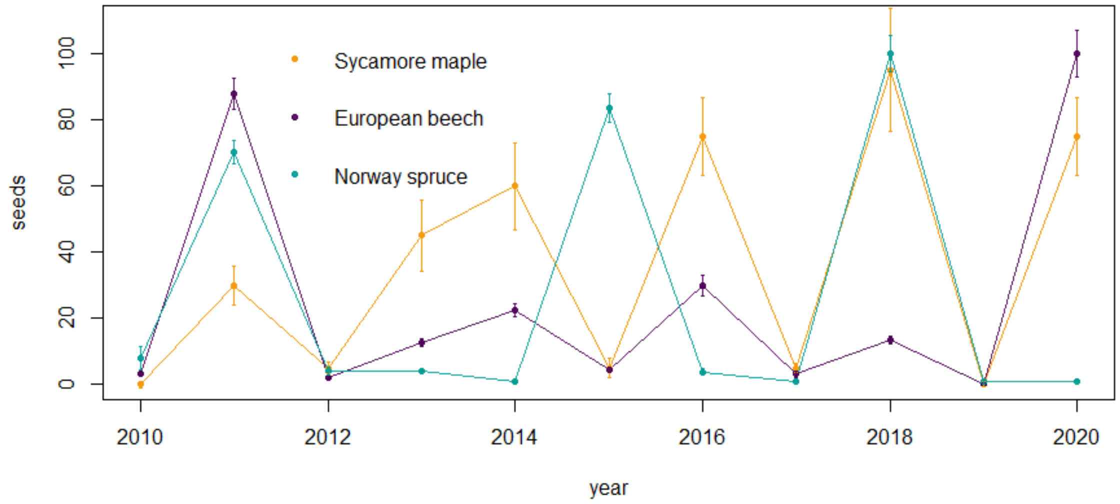

Figure 1: Standardised mean seed rain of Sycamore maple (Zöbelboden), European beech (Rothwald) and Norway spruce (Rothwald). Bars denote standard error.

This reproductive strategy termed *masting* results in occasional high seed production years interspersed by years of low or absent seed crops (Kelly 1994, Pesendorfer *et al.* 2021). Combined with the varying capacity to store surplus seeds to meet future demand, this behaviour may result in seed scarcity for restoration and afforestation efforts - especially for recalcitrant species with a short viability period (Burkart 2018, Konrad *et al.* 2023). As seed harvesting is labour- and time-intensive, predicting seed crops would support planning and resource allocation within the seed, forestry and restoration sectors (Pearse *et al.* 2021, Kettle *et al.* 2010). Furthermore, as climate change may lead to a breakdown in masting patterns (Foest *et al.* 2024) and an increase in the prevalence of biotic pests (Ciceu *et al.* 2024), the issue of seed (non-)availability has become a matter of urgency (Hazarika *et al.* 2021).

Seed production also plays an important role in wildlife management (Elliott & Kemp 2016) and public health risk anticipation (Rubel & Brugger 2020, Bregnard *et al.* 2021), as it drives interannual variation in a range of community and ecosystem-wide processes in forests (Jones *et al.* 1998, Levine & Murrell 2003, Nopp-Mayr *et al.* 2012, Michaud *et al.* 2024). For instance, forecasting acorn crops or failures could reduce the potential for human-bear conflicts in Japan (Oka *et al.* 2004*)*, aid planning of release time for endangered seed-dependent animals (Fidler *et al.* 2008), and provide earlier anticipation of peak infection risk for tick-borne diseases (Rubel & Brugger 2020). Therefore, improving our understanding of seed production patterns and developing short-term and long-term predictions of seed production represents a high priority in forest ecology and beyond (Journé *et al.* 2023).

Forecasting of ecological time series relies on quantitative or mechanistic models that capture the intrinsic and extrinsic drivers of spatiotemporal variation in the phenomenon of interest, usually based on historical observations (Dietze *et al.* 2017, Lewis *et al.* 2022). In tree seed production, the strong relationship with weather before and during flowering and seed development provides a unique opportunity to develop anticipatory predictions of seed crop size months or even years in advance (Pearse *et al.* 2021). For example, summer temperatures two years before can act as a cue for synchronizing flowering effort in some *Fagus* species (Piovesan & Adams 2001, Vacchiano *et al.* 2017), while spring temperature and precipitation can influence pollination and acorn maturation processes in *Quercus* species (Perez-Ramos *et al.* 2010, Fleurot *et al.* 2023). Therefore, identifying key weather patterns that correlate with seed production allows for hindcasting and subsequent forecasting (Journé *et al.* 2023).

While several studies have identified specific time windows and weather patterns which correlate strongly with annual seed production in a given species (Poncet *et al.* 2009, Koenig *et al*. 2015, Bisi *et al.* 2016, Moreira *et al.* 2021), few have explored the cumulative effect of these time windows on the sequential processes that ultimately determine the extent of annual seed production, from bud initiation over flowering and pollination to seed development, fructification, and abscission. This sequential approach provides important information about the predictability of a system (Pennekamp *et al.* 2019) as well as the potential forecasting horizon, the time over which useful forecasts can be made (Petchey *et al.* 2015). Transforming earlier studies on correlations of weather and seed production into actual ecological forecasting is thus timely and promising.

The utility of a forecast can only be determined from the perspective of potential users, i.e. whether a forecast is accurate, precise, and early enough to generate or modify actions within the tree seed sector. This threshold is typically based on an agreed measure of forecasting proficiency. For instance, the weather forecast horizon is typically a few days ahead, while the forecast horizon for tree seed production is still largely unknown (Journé *et al.* 2023). Within the Austrian seed sector, actors have identified the value of a reliable prediction the year before seed rain, but any reliable forecast before summer of the seed harvest year would improve their planning horizon (Gadermayer July 2024, *pers. comm.*). From a biological point of view, this seems realistic for those species that show a strong alternating pattern (e.g. *Abies alba*) or species that exhibit “flower masting”, i.e. those that regulate their seed production mainly by variation in the number of flowers, which is usually determined by cues in the previous growing season (Pearse *et al.* 2016). Conversely, fruit maturation masting species - where the variation in seed production is due to differences in the rate of flowers maturing into seeds - might have a shorter forecasting horizon, as driving factors for variation operate mainly within the seed maturation year. Furthermore, any otherwise reliable prediction may be rendered incorrect by environmental vetoes that occur late in the fruit development cycle, such as extreme drought during the seed maturation phase which leads to fruit abortion (Nussbaumer *et al.* 2020).

Recently, Journé *et al.* (2023) used a sequential modelling approach to build hindcasting models for reproduction across 94 European beech (*Fagus sylvatica* L.) populations, in which they investigated how much variance can be explained as the sequence of biologically-relevant weather time windows gets closer to the actual seed production event. They found that the amount of explained variation increases strongly about one year before seed rain, providing a first estimate of a potential forecasting horizon at which meaningful predictions may be formulated. For most tree species, however, the explanatory power of the statistical relationship between weather and seed production, based on additive, sequential models suitable for forecasting, has not been explored.

Here, we use long-term, high-resolution data sets on annual seed production (hereafter "ASP") in six European tree species recorded in two Austrian old-growth forest sites to hind- and forecast seed production based on weather data. In addition, we included temporal autocorrelation with previous ASP data, which is indicative of intrinsic drivers such as resource dynamics (Sork *et al.* 1993, Pearse *et al.* 2016). Specifically, we constructed sequential statistical ASP models for three coniferous species, Silver fir (*Abies alba*), European larch (*Larix decidua*), and Norway spruce (*Picea abies*), and three broadleaved species, Sycamore maple (*Acer pseudoplatanus*), European beech (*Fagus sylvatica*), and European ash (*Fraxinus excelsior*), for some of which the weather correlations with seed production are poorly understood. Using a sliding-window approach and model selection (R-package *climwin*, van de Pol *et al.* 2016, Bailey & van de Pol 2016) based on weekly weather data, we investigate the change of explained variance with decreasing time horizon before seed rain. We developed our models using seed data until 2021 and forecast seed amount for the following four years, including the fall of 2025. Thus, we demonstrate what is possible by using sequential statistical ASP models and explore unchartered terrain by forecasting the upcoming ASP for six temperate European tree species. We aim to lay the foundation for further development of ASP forecasts, including tools designed for use by practitioners, as well as providing a first benchmark for the field.

Methods

Sites

We used ASP data from two montane old-growth forest sites in the Northern Limestone Alps in Austria, covering 18 years (Rothwald) and 30 years (Zöbelboden). Despite their proximity (50 km), the sites differ slightly in species composition, climate, and soil properties. For detailed site descriptions, see Supplementary Information.

Data

Both study sites are equipped with rodent-safe seed traps (detailed description of Rothwald in Gratzer *et al.* 2022). At Zöbelboden, 56 traps are arranged across 14 locations throughout 90 ha. We used data from Zöbelboden covering ASP of *Picea abies, Fagus sylvatica*, *Larix decidua*, *Acer pseudoplatanus* and *Fraxinus excelsior* from 1994 to 2022, and data from Rothwald for ASP of *Picea abies, Fagus sylvatica* and *Abies alba* from 2006 to 2023.

We used downscaled weather data on air temperature and precipitation from existing datasets or interpolated data from nearby weather-stations using statistical methods in daily resolution. These high-resolution datasets provide more accurate results especially in such mountainous terrain with steep temperature gradients. A detailed description of the method can be found in Lehner *et al.* (2024) and Gadermaier *et al.* (2024).

Data manipulation

First, we calculated the mean annual seed rain/m^2 per species and site. As the species distribution at Zöbelboden is uneven, we only included traps with cumulative seed rain values above the 10th percentile for each species, in order to exclude spurious seed dispersal events. For Rothwald, we used seed data of spruce and fir from the conifer-dominated basin, and beech seed data from the beech-dominated slopes.

We aggregated the daily weather data to mean weekly temperatures and weekly precipitation sums. To incorporate the combined effect of these two factors, we calculated the weekly climatic water balance (CWB) following the Penman-Monteith equation within the R-package *Evapotranspiration* (version 1.16, Guo *et al.* 2022).

Data analysis

To investigate the relationship between ASP and previous weather conditions, we used a sliding-window approach to model selection, namely the package *climwin* (version 1.2.3; Bailey & van de Pol 2016), specifically the function *slidingwin()*, which was designed for investigating correlations of varying-length windows of a given time series to any biological variable of interest (Bailey & van de Pol 2016). S*lidingwin()* uses deltaAIC as measure of comparison to a previously constructed null model (Bailey & van de Pol 2016), with the AIC being a common criterion for the goodness of model fit (Burnham & Anderson 2002). Assuming that autocorrelation would play a significant role in ASP variation, we constructed a null model using prior ASP (seeds$_{T-1}$) as a fixed effect.

Slidingwin() requires a fixed date for the biological variable in question; we chose the first day of week 36 (early September) as seed rain date, corresponding roughly with the time when seed harvest usually commences (Bailey & van de Pol 2016). Although *climwin* has been designed as a model selection tool, it does not allow for constructing sequential additive models. To implement this approach, we used *slidingwin()* to identify relevant time windows, and then modelled their sequential additive effects (Fig. 2). Based on literature, we considered prior ASP and weather windows up to two (three for *Larix decidua*, Haasemann 1973) years before seed rain as predictors for subsequent ASP. Note that no prior knowledge of likely weather windows within this time frame was assumed.

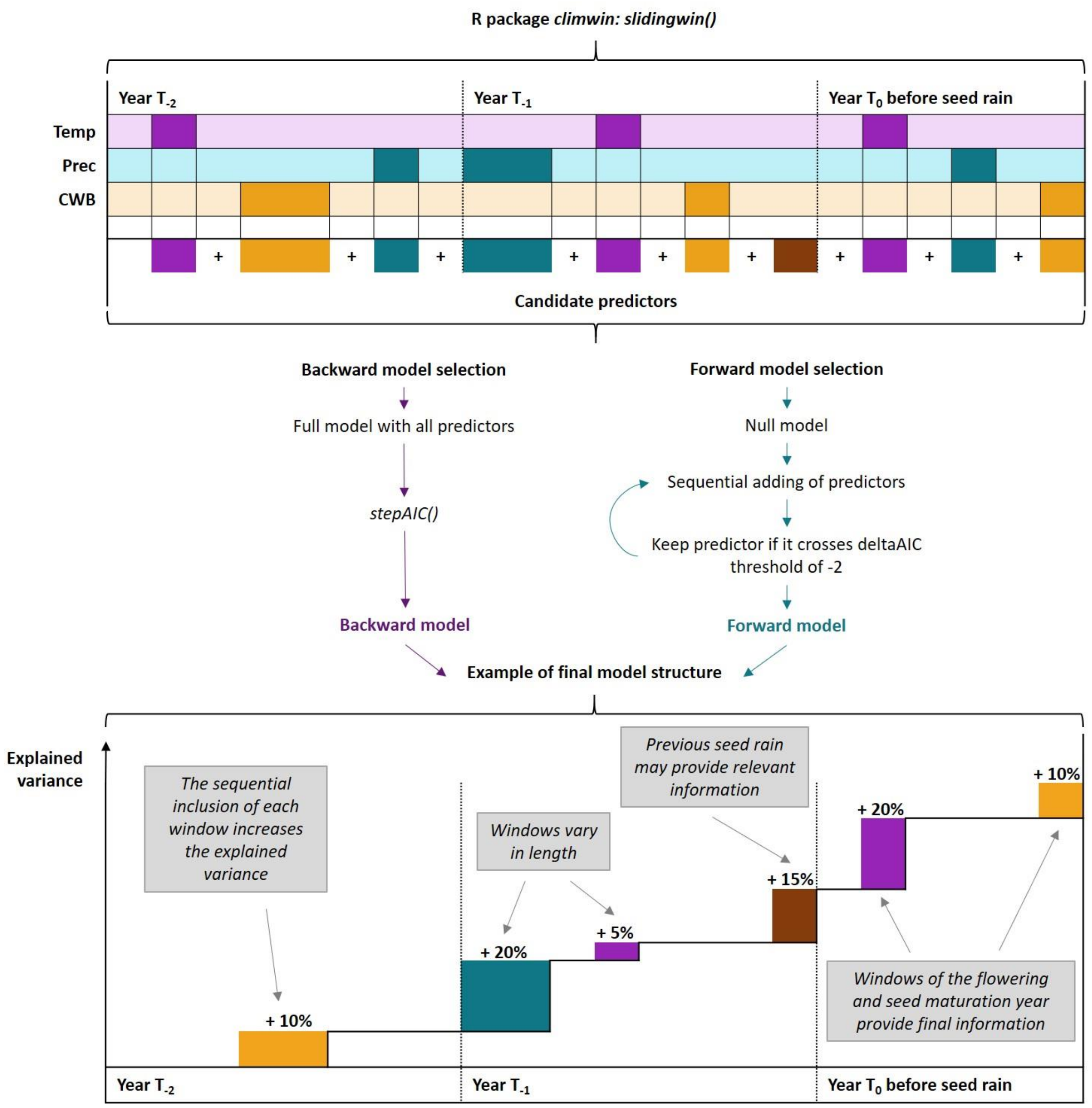

Figure 2: Schematic depiction of species- and site-specific model building: First, we used *slidingwin()* to identify the start and end of the candidate weather predictors (Temp = mean weekly temperature, Prec = weekly precipitation sum, CWB = climatic water balance). We used I) AIC-based stepwise regression for backward model selection, and II) conservative forward model selection by adding predictors in their natural sequence, keeping them only if they provided at least an improvement in AIC of -2 over the previous best model (null model: seeds ~1).

To build species- and site-specific versions of the sequential models, we standardised mean ASP between 0 and 100. Within our ASP time series, assumptions of negative binomial distribution were verified (Zuur *et al.* 2009), so we fitted negative binomial generalized linear models using a log link (R-package *MASS*, v. 7.3-53, Venables & Ripley 2002).

For backward model selection, we built a full statistical model of all candidate windows for each species and site and then used *stepAIC()*. We allowed for overfitting and collinearity of predictors, as we were explicitly focused on site- and species-specific statistical modelling, rather than hypothesis testing (Dormann *et al.* 2012). Furthermore, to reflect the realistic availability of information for future forecasting application, we conducted a second, conservative approach of forward model selection. Here, we started with a null model of standardised mean ASP ~ 1 and then added the earliest weather predictor that would become available. We assessed whether it improved model fit (deltaAIC > 2), otherwise we dismissed it. We progressed through all predictors, and then used *stepAIC()* to check whether removal of any predictor would further improve the AIC. The resulting model was termed the “forward model”, as opposed to the “backward model” resulting from the backward model selection.

We compared the results of both model selection approaches for hindcasting and used two novel approaches of investigating ASP model proficiency with regard to the forecast horizon. Finally, we predicted standardised mean ASP for 2022 to 2025. As the available high-resolution weather data was available until the end of 2023, we were limited in our forecasts to 2024 and 2025.

All analyses were conducted in R version 2023.03.0+386 (Posit team 2023).

Results

Overall hindcasting performance of models

As the period between hindcast and seed rain narrows, the increase in explained variance along the temporal sequence of added model predictors (Fig. 3) reflects a decline in prediction uncertainty. The overall final model performance was higher for backward selected models than for forward selected models. For backward selection, the adjusted Kullback-Leibler R^2 (Cameron & Windmeijer 1997, Zhang 2022) of final models ranged from 0.47 (Sycamore maple Zöbelboden = ZB) to 0.97 (Silver fir Rothwald = RW), while forward selection resulted in a wider range from 0.23 (European ash ZB) to 0.92 (Silver fir RW). Models derived from the shorter ASP time series (RW) resulted in higher R^2, while model performance of ZB was more diverse.

All models except one achieved an R^2 of at least 0.3 [max. 0.93] within the year before seed rain (T-1), indicating sufficient information was available to explain a major part of the total seed rain variation. However, weather predictors of the seed rain year T0 further increased R^2, especially for beech, spruce and larch (Fig. 3, Table 1).

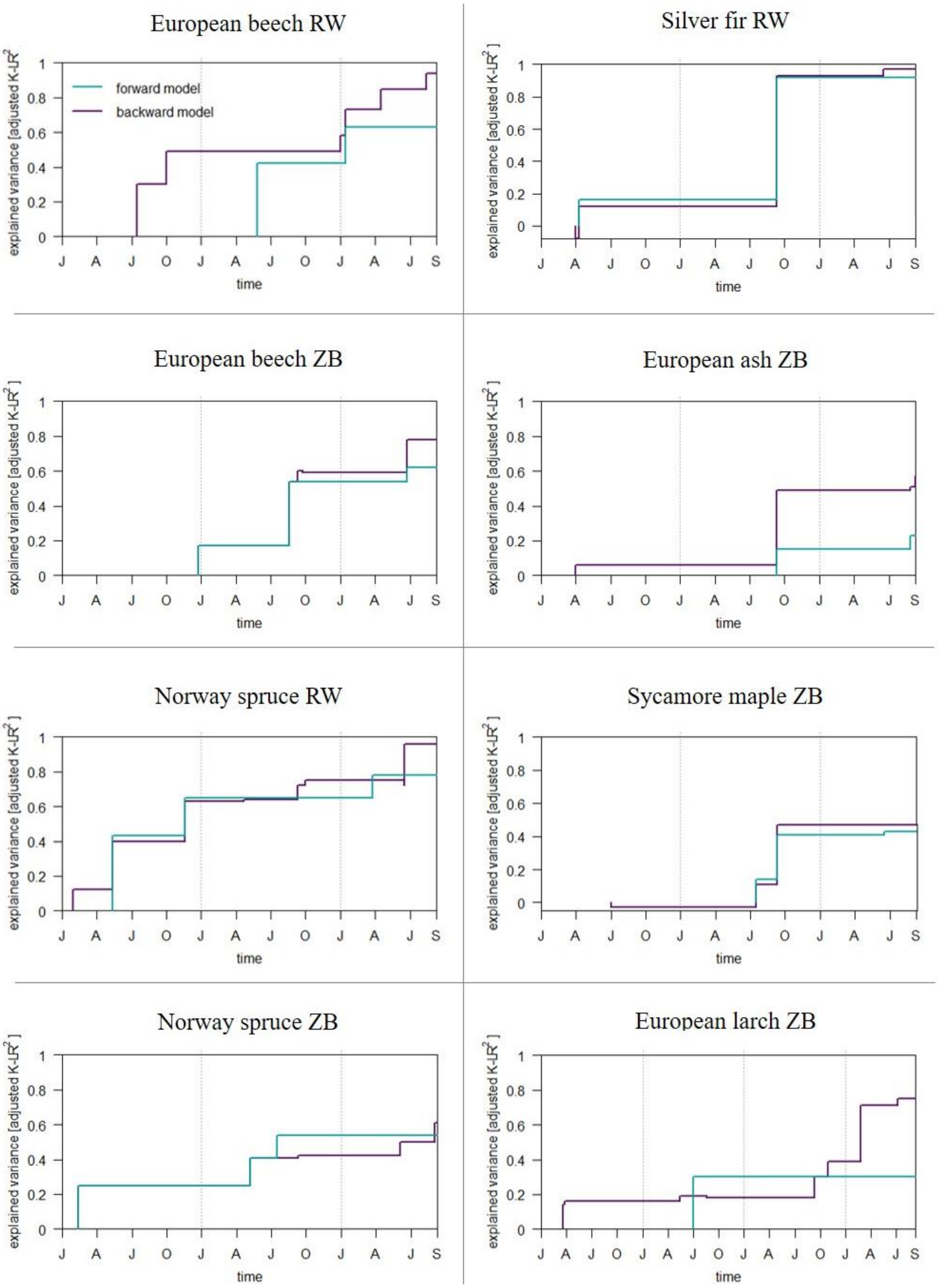

Figure 3: Evolution of the adjusted K-L R^2 per added predictor within the final models of the forward (turquoise) and backward (purple) selected models. The right end of the x-axis represents the time of seed rain in early September. Toward the left side of each plot, the dotted vertical lines delimit the previous two years (or three in the case of larch) with every third month abbreviated (first J = January, A = April, second J = June, O = October).

Model accuracy and bias

Despite the high proportion of explained variance in most models, the RMSE remained high (from about 20 to 45, see SI). As all seed data are scaled between 0 and 100, this indicates continuous average prediction errors of 20% to 45%. To examine the development of model accuracy over time, we assessed the percentage of cases where the prediction interval (prediction ± SE) and the observation interval (observation ± SE) overlapped along the model sequence (prediction-observation interval coverage, POIC). Table 1 shows R^2 and POIC of T-1 and T0. An increase in R^2 from T-1 to T0 is mostly associated with an increase in POIC, and only rarely with a decrease in T0. Thus, we see an increase in model accuracy as the seed rain approaches that is reflected by the increase in R^2 in Figure 3.

Table 1: R^2 and prediction-observation interval coverage [%] of each final forward (“for”) and backward (“back”) selected model at the end of the year before seed rain (T-1) and at the end of the seed rain year (T0). The absence of further predictors added in T0 is marked by “-“.

Species and Site	**T-1**		**T0**	
	R^2	**POI Coverage [%]**	**R^2**	**POI Coverage [%]**
Beech RW back	0.58	46.7	0.94	66.7
Beech RW for	0.42	46.7	0.63	40
Beech ZB back	0.59	40.7	0.78	37
Beech ZB for	0.54	25.9	0.62	29.6
Spruce RW back	0.75	73.3	0.96	80
Spruce RW for	0.65	33.3	0.78	53.3
Spruce ZB back	0.42	40.7	0.61	44.4
Spruce ZB for	0.54	29.6	-	-
Fir RW back	0.93	80	0.97	86.7

Fir RW for	0.92	46.7	-	-
Larch ZB back	0.39	42.3	0.75	61.5
Larch ZB for	0.3	28.5	-	-
Ash ZB back	0.49	55.6	0.57	63
Ash ZB for	0.15	29.6	0.23	44.4
Sycamore ZB back	0.47	63	-	-
Sycamore ZB for	0.41	55.6	0.43	55.6

To clarify whether the remaining inaccuracies are biased in a particular direction, we used prediction-observation plots (Fig. 4) to visualise which models tend to over- or underpredict seed rain. The close alignment of the predicted vs. observed line with the 1:1 line in Figure 4 indicates that most models show unbiased, but partly imprecise, predictions already in the year before seed rain (T-1). Some models tend to underpredict seed production in T-1 (forward models for larch, ash and beech). Overall, the most common bias is underprediction in T-1 and minor over- and underprediction in T0. Forward models also tend to have a slightly larger bias than backward models, consistent with Table 1. In T0 models for ash and spruce, the bias varies with model selection approach.

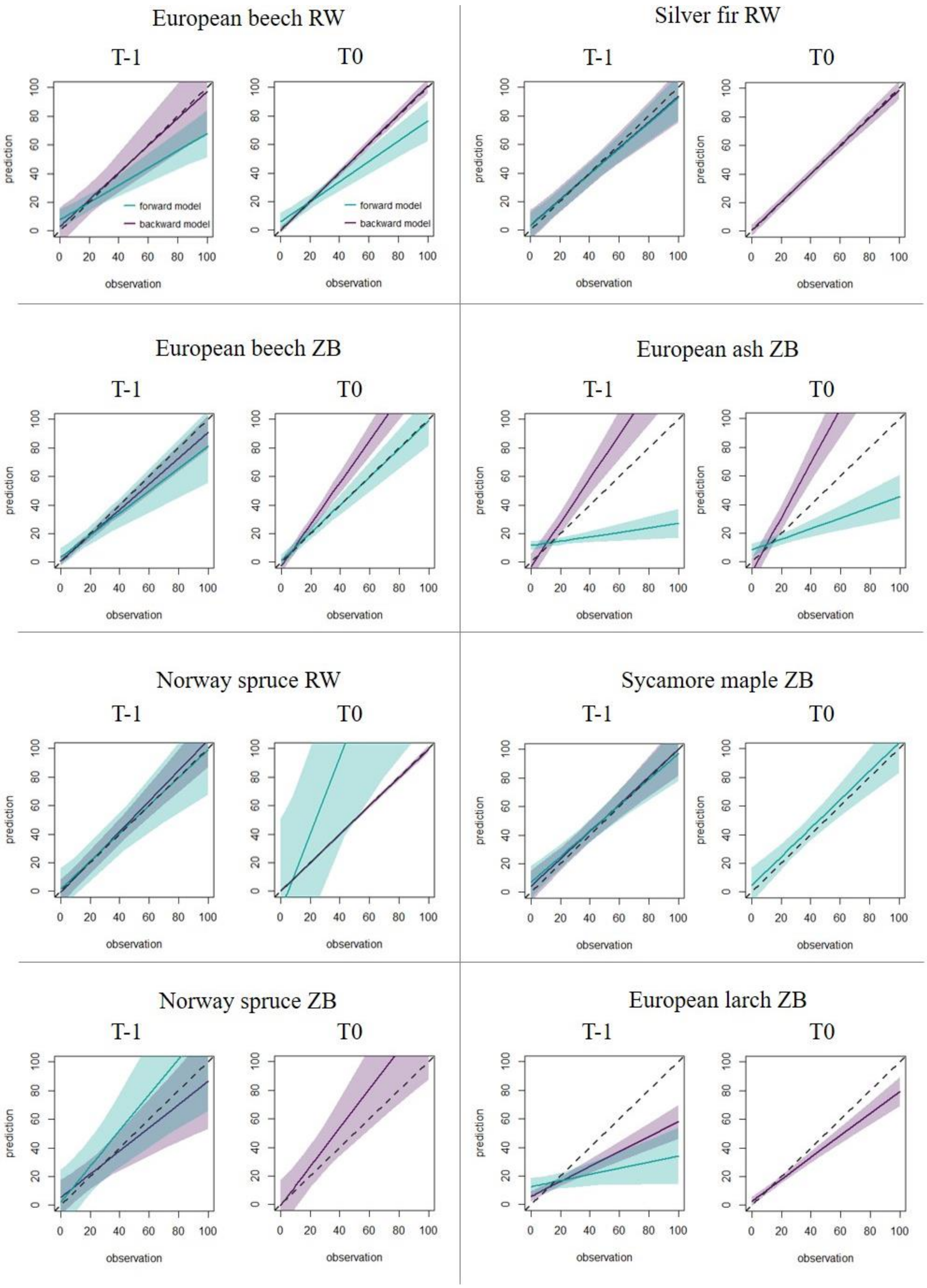

Figure 4: Linear models depicting the relationship of predictions vs. observations with a 95% confidence interval (shaded area) of the forward (turquoise) and backward (purple) selected models, once at the end of the year before seed rain (T-1) and once in the year of seed rain (T0). The dotted line represents the 1:1 line.

Model structure and components

Previous ASP explains a large proportion of the variation in most models for fir, ash, and maple, and only a small proportion (< 0.15 R^2) in most models for beech, spruce and larch. In the forward selected models for spruce and larch, as well as in all RW models for beech, the previous ASP is absent (see SI). Overall, forward selected models suffer less from multicollinearity and are more stable than backward selected models, which were deliberately allowed to be overfitted. Accordingly, forward selected models tend to have a much lower number of predictors. The final model weather predictor types are diverse, although most windows fall in the first half of the calendar years, between late winter and early summer.

Exploring the potential forecasting horizon

The potential forecasting horizon depends on the formulation of a measure of this “usefulness”, which will vary according to the user group. By investigating the change in explained variance (R^2) and prediction-observation interval coverage (POIC), we have provided initial estimates of the quantitative limits of potential forecast horizons for each species.

To assess the categorical hindcasting capability of our models, we sorted seed rain data into 3 categories: <=10%, >10% and >50% of the seed rain maximum. These were informed by opinions from the Austrian tree seed sector, and might represent seed production failures, moderate and bumper seed crops. Most seed years fell into the lowest category and very few into the highest. We compared the T-1 and T0 year predictions of each model selection approach: Hindcasting above 10% of the maximum worked well for all species in the year prior to seed rain. Hindcasting “lows” in T-1 worked well for beech, spruce, fir and ash, while for larch and maple less than two third of the categorical predictions were accurate

(Table 2, Fig. 4). In line with R^2 and prediction-observation interval coverage (Table 1), we see that model accuracy tends to be higher for backward selected models.

Table 2: Proportion of correct (hindcast) predictions of seed amount categories in % of each final forward ("for") and backward ("back") selected model at the end of the year before seed rain (T-1) and at the end of the seed rain year (T0).

	T-1			**T0**		
Category	**0-10**	**>10**	**>50**	**0-10**	**>10**	**>50**
Beech RW back	100	88	100	100	100	100
Beech RW for	29	75	50	57	75	100
Beech ZB back	95	71	100	100	86	100
Beech ZB for	95	71	100	95	71	100
Spruce RW back	91	100	100	100	100	100
Spruce RW for	82	100	67	91	100	33
Spruce ZB back	82	80	67	88	80	100
Spruce ZB for	94	90	67	-	-	-
Fir RW back	100	100	100	100	100	100
Fir RW for	100	100	80	-	-	-
Larch ZB back	65	78	50	82	89	50
Larch ZB for	65	78	50	-	-	-
Ash ZB back	83	100	100	100	89	100
Ash ZB for	44	100	0	78	89	0
Sycamore ZB back	56	94	83	-	-	-
Sycamore ZB for	56	94	83	67	94	83

Forecasting

Using the most accurate hindcasting models, we forecast seed rain for 2022 to 2025 for all six species (Fig. 5). Testing the envisioned forecast horizon, categorical predictions were correct for beech, maple and larch, mixed for spruce and fir, and incorrect for ash one year in advance. Notably, the model for Silver fir, which showed the best overall hindcasting performance, failed to correctly predict ASP when it encountered a pattern of consecutive high ASP years in 2021 and 2022, outside the variation in the training dataset (which contained no instances of consecutive high ASP). Final model predictions (including predictors of the seed year) were mostly categorised correctly in maple, ash and larch, with mixed performance in fir, beech and spruce (for further details, see SI). Forecasts for 2024 onwards are currently limited both by seed and weather data and will thus be updated after seed sampling and availability of 2024 weather data.

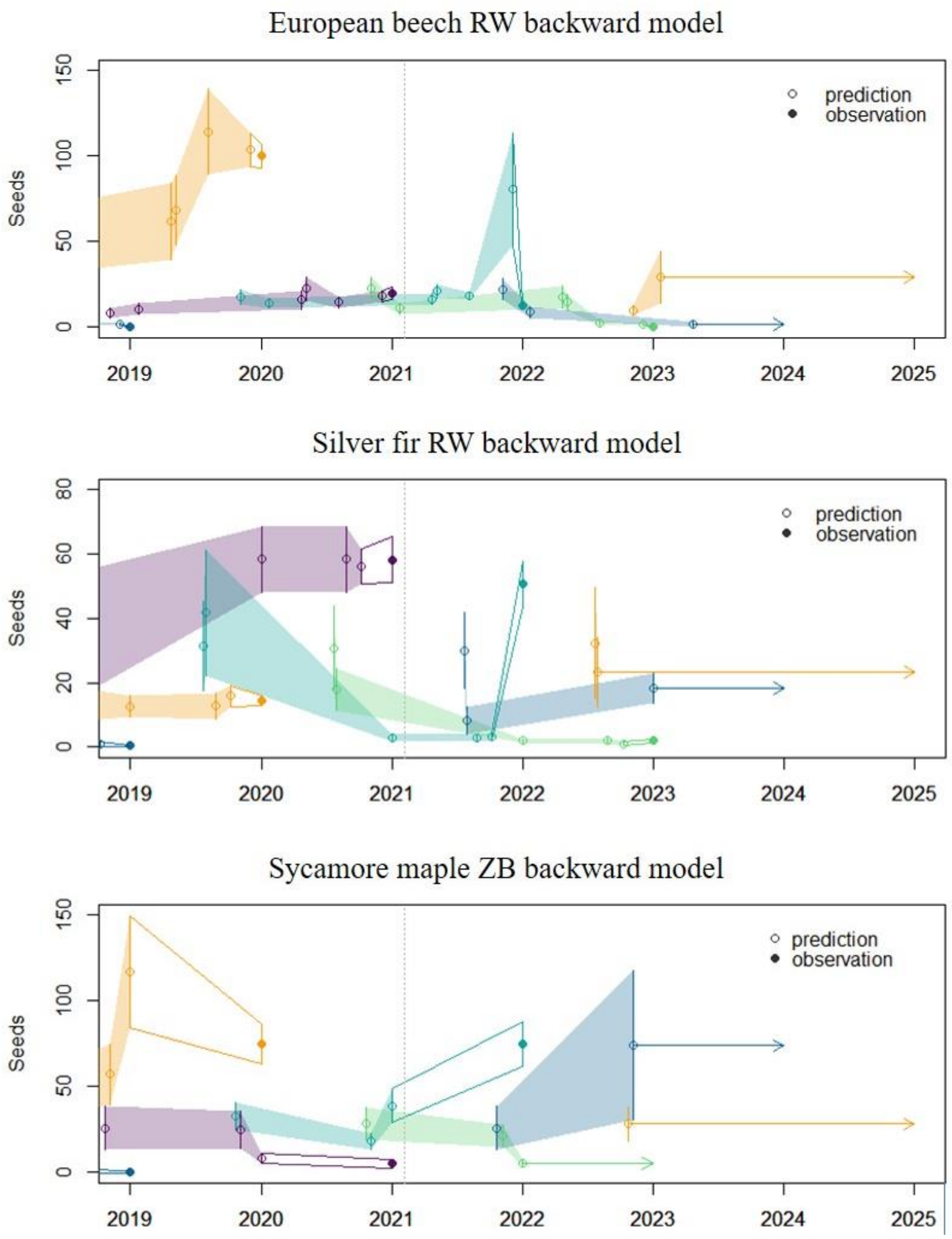

Figure 5: Sequential backward model predictions for European beech RW, Silver fir RW and Sycamore maple ZB. Empty circles represent predictions with standard error of prediction. Full circles represent actual observations with according standard error. The dotted vertical line marks the boundary between hind- and forecasting. Colours mark individual year predictions of the sequential models.

Discussion

Annual seed production (“ASP”) in species with high interannual variability and spatial synchrony (masting) is predictable based on weather and previous ASP, with a forecast horizon that holds value for the tree seed sector. We explored the potential for forecasting ASP of six tree species, for only one of which forecasts have been developed previously. Furthermore, ASP of maple and ash has not been studied in relation to weather, to the best of our knowledge. Our results indicate that ASP of some species can be predicted already in the year prior to seed rain. The currently achieved model performance may be beneficial for seed harvesters, nurseries and forest and wildlife managers.

Our models are based on correlations of weather and ASP data. While correlations do not imply causation, some may possess biological significance. The majority of the final weather predictors within this study fall between late winter to early summer, consistent with previous studies (Matthews 1955, Moreira *et al.* 2021). However, limited understanding of species-specific physiological processes and their timing hinders the distinction of statistical artefacts and biologically meaningful periods. Here, close monitoring of the species-specific relationship of weather and reproductive phenology would allow for more advanced modelling, i.e. moving from a calendar-based approach to a standardised assignment of a phenological ID (“pheno-id”) to each week, i.e. dating weather windows according to the annual timing of key phenological events, rather than windows fixed to calendar dates. Such models may allow generalised models to be used in the absence of local training data and may help explain the site-specific weather windows we found for spruce and beech, potentially providing further insights into tree reproduction physiology. For our current undertaking, we relied on weekly calendar-id, as the calendar year aligns with the course of both light availability and key solar events to which plants appear to be sensitive, as was recently found for the summer solstice (Journé *et al.* 2024).

Previous ASP explains a large part of the variation in models for fir, ash and maple, and less for beech, spruce and larch. This fits previous work showing that high ASP correlates with reduced syrup yield in *Acer saccharum* (Rapp & Crone 2015) and decreased tree ring growth in ash (Bochenek & Eriksen 2010), suggesting that these species may alternately invest in growth and reproduction (resource-switching, Pearse *et al.* 2016). Regarding fir, the first attempt to predict seed rain in 2022 failed due to the previously unobserved occurrence of two consecutive high seed years.

A strong dependence on previous ASP may fix the theoretically accomplishable forecasting horizon to 12 months. In reality, high-quality seed production monitoring typically requires several months for full sample measurement and validation, making data latency one of the fundamental challenges in predicting ASP. Combining seed sampling methods with different levels of accuracy to reduce latency is a promising way forward.

Establishing new seed monitoring projects and ensuring the future of existing ones may be just in time to understand existing relationships between weather and seed production, and to anticipate their future development. Trees may struggle to adapt to climate change, leading to disruptions in seed production and recruitment, either directly or indirectly (Bogdziewicz *et al.* 2024, Foest *et al.* 2024). The increasing occurrence of environmental vetoes, such as spring frosts or summer droughts (Nussbaumer *et al.* 2020), will inevitably disrupt forecasts. Monitoring these vetoes alongside forecasting and seed sampling is crucial for understanding future vulnerability and recovery, and for building trust with the communities concerned (Bodner *et al.* 2021). Within the tree seed sector, forecasts will mainly inform harvesting activities (in forest stands and orchards) but also seed orchard management actions like pruning, irrigation, and fertilisation.

Current practices of observing flowering effort provide valid estimates before seed harvest for flower masting species (Pearse *et al.* 2016). Therefore, a forecast one year in advance has the opportunity for major updates before seed rain: the actual observation of flowering and the weather conditions during flowering, seed formation and seed maturation. This can be incorporated into the forecast communication, both in terms of refining the prediction and its uncertainty. It must be clear what the forecasts are based on and how often they have been correct in the past at the given forecast horizon. Throughout spring, information on flowering effort should be incorporated, and it must be emphasised that rare and localised weather events can disrupt ASP in a particular forest area.

Discussions with people working in the tree seed system indicate a preference for categorical forecasts, but we are still working to understand the needs of potential user groups. Different thresholds may determine the individual effort to harvest seed of a given species in a given year, depending on species (market) demand, storability, and seed stocks, individual strategies and economic constraints. For this study, besides exploring the forecasting horizon with a quantitative precision-oriented metric (POIC), we have assumed that the main difference is whether some (>10%) or none (<=10%) of the seeds will be available, and whether there is likely to be an exceptionally high seed year (>50%). It can be reasonably argued that each of these predictions would result in different actions and planning behaviour, although some highly demanded and subsidised species are likely to be harvested at similar intensities whether the yield is predicted to be "just above zero" or exceptionally high (Konrad *et al.* 2023).

Despite natural limitations, ASP appears to be predictable with a promising, though imperfect, degree of accuracy for most studied species roughly one year in advance. Future forecasting efforts should prioritise species based on lack of storability, coupled with demand, which in turn should be driven by species resilience. Increased harvesting of rare species, regardless of seed storability, seems rational given the need to maintain and increase biodiversity in forest landscapes. Here, seed forecasts will provide an essential part for addressing climate change adaptation and mitigation.

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Author contributions

IO and MBP conceived the ideas and designed the study, IO conducted the analysis and wrote the manuscript with critical contributions from MBP, AHP and GG. GG, HK and SS provided data. All authors provided editorial input and gave final approval for publication.

Data availability statement

The datasets used in the study will be available at the Dryad repository after publication.

Conflict of interest statement

No conflicts of interest are declared.

Statement on inclusion

Our study benefits from collaboration with practice-orientated researchers at the Austrian Research Centre for Forests, and from being developed within a larger interdisciplinary project addressing issues with seed supply for forests in Central Europe. Consequently, the development of our forecasting models has been shaped through interactions with foresters and practitioners from the Austrian tree seed sector. For example, earlier versions of this work were presented and discussed at a 2-day workshop with people from harvesting companies, nurseries, orchard owners, the forest management of the Austrian Federal Forests and the Federal Administration in the summer of 2024, and feedback from that workshop has been incorporated into the present manuscript. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

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