Continental-scale evaluation of downy birch pollen production: Estimating the impacts of global change

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ABSTRACT

The high prevalence of hay fever in Europe has raised concerns about the implications of climate change-induced higher temperatures on pollen production. Our study focuses on downy birch pollen production across Europe by analyzing 456 catkins during 2019–2021 in 37 International Phenological Gardens (IPG) spanning a large geographic gradient. As IPGs rely on genetically identical plants, we were able to reduce the effects of genetic variability. We studied the potential association with masting behavior and three model specifications based on mean and quantile regression to assess the impact of meteorology (e.g., temperature and precipitation) and atmospheric gases (e.g., ozone (O_3) and carbon-dioxide (CO_2)) on pollen and catkin production, while controlling for tree age approximated by stem circumference. The results revealed a substantial geographic variability in mean pollen production, ranging from 1.9 to 2.5 million pollen grains per catkin. Regression analyses indicated that elevated average temperatures of the previous summer corresponded to increased pollen production, while higher O_3 levels led to a reduction. Additionally, catkins number was positively influenced by preceding summer's temperature and precipitation but negatively by O_3 levels. The investigation of quantile effects revealed that the impacts of mean temperature and O_3 levels from the previous summer varied throughout the conditional response distribution. We found that temperature predominantly affected trees characterized by a high pollen production. We therefore suggest that birches modulate their physiological processes to optimize pollen production under varying temperature regimes. In turn, O_3 levels negatively affected trees with pollen production levels exceeding the conditional median. We conclude that future temperature increase might exacerbate pollen production while other factors may modify (decrease in the case of O_3 and amplify for precipitation) this effect. Our comprehensive study sheds light on potential impacts of climate change on downy birch pollen production, which is crucial for birch reproduction and human health.

1. Introduction

The World Allergy Organisation (WAO) estimates that up to 40% of the world's population is sensitized to at least one allergen, while between 10 and 30% suffers from an allergy (Pawankar et al., 2013). Particularly in Europe, the prevalence of hay fever has increased substantially in the past (D'Amato et al., 2020) and may continue to rise with increasing levels of pollen production (Beggs, 2004; Damialis et al., 2019). In addition, future pollen loads, such as those from birch, are expected to change regionally in response to altered plant distribution driven by changing growing conditions under climate change (Rojo et al., 2021). Nowadays, the prevalence of allergic sensitization in Germany to the major allergen (Bet v 1) of birch (*Betula* spec.) is 18% (Beutner et al., 2021; Li et al., 2022). Examining potential environmental factors influencing pollen production is essential to estimate forthcoming changes. Therefore, plant individuals sharing identical genetic backgrounds can reveal environmental impacts, which are otherwise confounded by high inter-individual genetic variability (Ranpal et al., 2022).

The network of the International Phenological Gardens (IPG) includes a set of 23 plant species at 63 active IPGs across 19 European countries (Renner and Chmielewski, 2021). The peculiarity of this network is that every individual of a plant species was propagated vegetatively from a single mother tree, thereby eliminating genetic variability. The vast geographic extent of the network has been used to document large-scale temperature effects on plant phenology (Caffarra and Donnelly, 2011; Olsson et al., 2017; Linkosalo et al., 2019; Wenden et al., 2020) or to study the effects of biogenic volatile organic compound (BVOCs) emission patterns along the latitudinal gradient of these gardens (van Meeningen et al., 2016). The latitudinal and longitudinal gradients, which are covered by the IPG sites, present a valuable basis for investigating the impact of climate on plants through natural experiments (Frenne et al., 2013). Research on pollen production of allergenic plants, however, has not been applied so far in this unique network.

Birch is a wind-pollinated species that produces large amounts of pollen (Piotrowska, 2008; Geburek et al., 2012; Ranpal et al., 2022). Its pollen are, together with those of grass (Poaceae) species, the most common cause for allergic symptoms such as rhinitis and asthma (D'Amato et al., 1998; Biedermann et al., 2019). *Betula pubescens* Ehrh. (downy birch), frequently planted in the IPG network, is a tree species with a broad natural distribution across Europe, characterized by one of the most northerly and easterly distributions among European tree species (Beck et al., 2016). It can survive on compact soils and wet peatlands (Hynynen et al., 2010) and can be found at higher elevations and in European boreal forests (Beck et al., 2016). In addition, several varieties of birch are frequently cultivated as ornamental trees in temperate cities (Rojo et al., 2021).

Studies on birch flowering usually show a large year-to-year variation in the amount of male and female catkins and the produced pollen and seeds, respectively (Ranta et al., 2008), which is known as masting behaviour (Kelly, 1994). Aerobiological studies examining the amount of atmospheric birch pollen concentrations suggest that such masting events can occur every second (Latałowa et al., 2002) or third year (Detandt and Nolard, 2000). There is still only a limited understanding of the individual-specific pollen production of birch, its spatiotemporal patterns, and its response to environmental stressors. Previous studies have primarily focused on estimating birch pollen production within relatively small geographic areas (Jato et al., 2007; Ranpal et al., 2022) or along environmental gradients in urban (Jochner et al., 2013; Kolek, 2021; Jetschni et al., 2023) or mountainous regions (Ranpal et al., 2023). In general, especially higher temperatures and CO_2 concentrations were linked to higher levels of pollen production in various plant species (Ziska and Caulfield, 2000; Wayne et al., 2002; Albertine et al., 2014). Positive correlations were documented for previous summer's temperatures along an altitudinal gradient in non-masting years (Ranpal

et al., 2023). However, in two urban-rural gradient studies, birch pollen production was found to be negatively correlated to temperature (Jochner et al., 2013; Jetschni et al., 2023) as well as to foliar potassium and iron concentration and atmospheric NO_2 concentration (Jochner et al., 2013). In addition, it has to be considered that plant viral infections have an impact on the quantity of the birch pollen production, namely a significantly lower amount of pollen was found in catkins with virus infected pollen (Gilles et al., 2023). These findings point to the fact that the relationship between pollen production and environmental factors is likely to be multifaceted, whereas not only a single stressor exerts an influence on pollen production. Different levels of urbanisation and air pollution may change the plant responses non-linearly, i.e., between central Europe (Germany) and the Mediterranean (Greece) (Damialis et al., 2011). We had previously reported considerable differences in pollen production among same-aged birch trees growing under similar microclimatic conditions in a small geographic area (Ranpal et al., 2022). While it is key to understand the influence of environmental factors for ascertaining the possible influence of climate change, only large-scale studies can fully capture the potential variability in birch pollen production in diverse environments. Detailed information on the factors affecting pollen production can help in developing models for pollen production prediction and in devising strategies to mitigate the adverse effects of allergenic pollen on human health.

In this study, we considered the effects of various environmental variables on pollen production of birch trees (2019–2021) planted in IPGs across Europe. Our aim was to obtain a more comprehensive understanding of the determinants of birch pollen production. Therefore, we carried out a detailed analysis of pollen production as a function of local environmental variables and accounted for the potential heterogeneity of the effects of the environmental variables across the conditional pollen production distribution.

2. Materials and methods

2.1. Study sites

This study was carried out during three consecutive years (2019–2021) at 37 IPGs located in eleven European countries (see Appendix Table 1). Catkin samples were obtained from up to 44 birch trees per year as some of the gardens had between one and three birch individuals.

The IPGs were located along a latitudinal gradient spanning over 2500 km, from Skopje, North Macedonia, in the Balkan region, to Trondheim, in northern Norway, and along a longitudinal gradient covering approximately 2000 km, from Glenveagh, Ireland, to Šiauliai, Lithuania (Fig. 1, Appendix Table 1). The largest distance between two

Table 1

Considered models (M) employing environmental variables of the previous summer: mean temperature ($Tavg_{t-1}$), precipitation sum ($PPsum_{t-1}$), ozone ($O_{3,t-1}$) concentration, carbon dioxide ($CO_{2,t-1}$) concentration and stem circumference (S_{cir}).

Models	Description	Independent variables
M1	Meteorology of previous summer	$Tavg_{t-1}$ and $PPsum_{t-1}$
M2	Meteorology and atmospheric gases of previous summer	$Tavg_{t-1}$, $PPsum_{t-1}$, $O_{3,t-1}$ and $CO_{2,t-1}$
M3	Meteorology, atmospheric gases of previous summer and stem circumference	$Tavg_{t-1}$, $PPsum_{t-1}$, $O_{3,t-1}$, $CO_{2,t-1}$ and S_{cir}

The explanatory variables considered in the models included mean air temperatures ranging from 13.8 °C (Trondheim, Norway) to 22.8 °C (Skopje, North Macedonia), total precipitation ranging from 69 mm (London, UK) to 462 mm (Bergen, Norway), ozone concentration levels ranging from 51.0 µg m^{-3} (Trondheim, Norway) to 90.8 µg m^{-3} (Freyung Waldhäuser, Germany), and CO_2 concentration levels ranging from 405.05 ppm (Šiauliai, Lithuania) to 413.04 ppm (Waldfeucht, Germany).
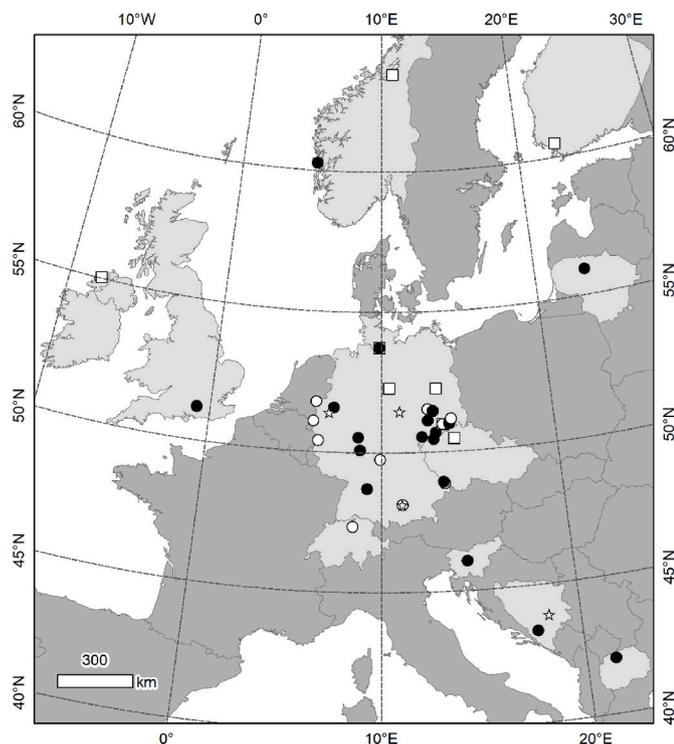
Fig. 1. Location of International Phenological Gardens across European countries. Circles are the IPG trees identified as clone 1, squares are identified as clone 2, stars are identified as clone 3 and black points represent other individuals with unique genotypes. Some circles/squares are overlapped. Light grey countries are included in this study.

IPGs was 2600 km (Skopje, North Macedonia to Glenveagh, Ireland). The shortest distance was 7.2 km (Freyung-Schönbrunn and Freyung-Waldhäuser, Germany).

Almost all selected IPG birches are within the natural distribution range of *B. pubescens*, as mapped by the European Commission Joint Research Centre (Caudullo et al., 2017), except trees from Bosnia and Herzegovina (Mostar and Sarajevo) and North Macedonia (Skopje). The trees in Bosnia and Herzegovina are the youngest, as they were planted in 2013 and 2014, respectively. The oldest trees are from Stuttgart (Germany), Tharandt-Hartha (Germany), and Ljubljana (Slovenia), which were planted in 1960.

2.2. Assessment of genetic identity

The IPG network was initially designed to only include individuals sharing the same genetic background (Schnelle and Volkert, 1957). However, this could not be maintained for all individuals of one plant since propagation methods and sites (mother gardens) changed in the past (Renner and Chmielewski, 2021). It is evident that propagation by cuttings is more favourable compared to grafting since the latter method is prone for a failed propagation, for example when the stock, which derives from another plant, gets dominant over the scion of the plant that should be propagated (Renner and Chmielewski, 2021). We used cambium samples from the twigs of which the inflorescences were obtained to determine the genetic identity of the trees. Genotyping was performed by the Bavarian Office for Forest Genetics (AWG; Teisendorf, Germany) at eight microsatellite loci (four alleles per locus). The analysis revealed two major clones (clone 1 as circles and clone 2 as squares in Fig. 1) with ten individuals in each clone group. Other clones with unique genotypes had up to four individuals, whereas 14 birch trees were not associated to a replicate genotype. This can be probably attributed to a failure of the grafting method or to the fact that the sampled birches were mistakenly assigned to the IPG network.

2.3. Pollen extraction method and pollen production metrics

To obtain catkin samples from the birches located at the IPGs, we instructed the local phenological observers of the respective gardens. We maintained regular communication with each IPG, provided them with the sampling material that included a detailed manual (https://www.ku.de/fileadmin/150303/Forschung/PollenPALS/Instruction_manual_pollenPALS_5th_Edition.pdf) to ensure a standardization in the catkin collection process. Male catkins with mature and closed anthers were collected each year in spring, after catkin elongation was commenced and before anthesis. Catkins were collected from different branches at attainable heights (1.5–2 m a.g.l.) in all four cardinal directions. The number of catkins inside a 50 cm × 50 cm × 50 cm sample cuboid in the crown were counted and utilized for extrapolating pollen production from catkins to the crown volume. Once the samples were received via express shipping, they were immediately stored at −20 °C until they were processed in the laboratory.

Extraction of downy birch pollen grains from closed inflorescences was performed following the method of Damialis et al. (2011), with the modification described in Ranpal et al. (2022): one medium-sized inflorescence from each cardinal direction and per tree was selected, and the length and width (at the broadest point) were measured. The number of flowers of each catkin was counted, and the catkin was then immersed in a 10% KOH solution overnight. On the following day, the solutions were boiled at 120 °C for 10 min, and the soft catkin was mashed with a glass rod to extract the pollen. To prevent pollen from clustering, a bipolar solvent, glycerol (70%), was added to a volume of 20 mL, and safranin was applied as a stain. The mixture was homogenized by continuous stirring, and two aliquots (10 μL each) of each suspension were taken using a VITLAB® micropipette. The samples were placed on microscope slides, covered with slips, and counted using a 100× magnification (Zeiss AXIO Lab.A1, Germany). The extraction method was repeated on another catkin of the same tree when there was a substantial difference between the pollen counts obtained from these two slides (>30%).

2.4. Meteorological data

The meteorological data used in this study were obtained from the E-OBS dataset (version 23.1e) from the EU-FP6 project UERRA (http://www.uerra.eu), the Copernicus Climate Change Service, and the data providers in the ECA&D project (https://www.ecad.eu) as documented by Cornes et al. (2018). These data are based on daily gridded values of meteorological variables, including mean, minimum, and maximum temperatures, relative humidity, precipitation, and global solar radiation. The dataset is based on a high-resolution 0.1° regular grid, which ensures accurate and detailed representation of meteorological variables. As catkins of the subsequent year develop during the preceding summer (Dahl and Strandhede, 1996), we considered the meteorological data of the previous summer. We aggregated (averaged or summed up in case of precipitation) the daily data for the period June to August. Relative humidity and sum of global radiation were excluded for further analyses due to their high correlations ($r > 0.6$) with temperature.

2.5. O_3, NO_2 and CO_2 data

Average data for ozone (O_3 at surface in μg m^{-3}), nitrogen dioxide (NO_2 at surface in μg m^{-3}) and atmospheric carbon dioxide (CO_2 column mean molar fraction in ppm) concentrations were derived from Copernicus Atmosphere Monitoring Service (CAMS) reanalysis. For O_3 and NO_2, monthly files containing 1-hourly analyses with a horizontal resolution of 0.1° × 0.1° were obtained. In case of CO_2, the available monthly data of 0.75° regular grid was used. We calculated mean values of the previous summer from the obtained data. NO_2 was excluded as it showed a high correlation ($r > 0.6$) with temperature.

2.6. Stem circumference

We included stem circumference as a proxy for the age of the tree. We inserted this variable since it was most accurately measured compared to alternative information such as tree height or planting year. For the former, a photograph with a measuring rod (as reference) placed in front of the trunk was used for deriving estimates; for the latter, planting year (which is known) does not equate to tree age (which is not known).

2.7. Data processing and statistical analyses

2.7.1. Data processing

Although we found that the selected trees also derive from different genotypes, we decided not to discard any of the trees, but instead to modify our statistical analyses to account for heterogenous effects, which may also be driven by factors such as genetics. We investigated 93 samples, as we had to remove 21 samples from the dataset due to diseased trees and a very low pollen production. To estimate pollen production, we used the mathematical method described by Damialis et al. (2011) and calculated it for different scales. In brief, we calculated the number of pollen grains per catkin (P_{ca}) by multiplying the number of pollen grains observed on a microscope slide by the ratio of the suspension volume (in mL) to the sample volume taken (10 μL). Next, we determined the number of pollen grains per flower (P_{fl}) by dividing P_{ca} by the number of flowers per catkin (Fl). Finally, to estimate the number of pollen grains per volume unit (m^3) of crown (P_{vuc}), we multiplied P_{ca} by the ratio of the number of catkins per crown sampling unit (C_{su}) and the volume of the sampling unit (0.125 m^3).

We also analyzed the temporal pattern of pollen and catkin production based on a subset of the 93 samples. To account for potential masting effects, we only considered the trees for which pollen production metrics were available for all study years. This was the case for 20 trees (resulting in 60 samples), and we assigned those trees to three different groups: i.e., group 1 with maximum values of pollen or catkin production in 2019, group 2 with maximum values in 2020, and group 3 with maximum values in 2021.

2.7.2. Mean regression

We investigated the effect of the environmental variables on pollen production based on three different model specifications of the form

$$Y = X_1 \beta_1 + \ldots + X_P \beta_P + U. \tag{1}$$

In (1), Y denotes the pollen production metric, $\mathbf{X} = (X_1, \ldots, X_P)$ are the environmental variables and the stem circumference with corresponding coefficients $\beta_1, \ldots, \beta_P$, and U is an error term. We modeled the conditional expectation:

$$E(Y|\mathbf{X}) = X_1 \beta_1 + \ldots + X_P \beta_P, \tag{2}$$

and assumed $E(U|\mathbf{X}) = 0$. This requires that the systematic effect of the environmental variables on pollen production is captured by the right-hand-side of (2). Parameter estimates were obtained by least squares, where the residual sum of squares is minimized.

The employed model specifications are summarized in Table 1 and were contrasted in terms of interpretations and model selection criteria. Model M1 includes the meteorological variables mean air temperature ($Tavg_{t-1}$) and sum of total precipitation ($PPsum_{t-1}$) of June, July, and August of the previous year (or previous summer). Model M2 additionally includes mean concentrations of ozone ($O_{3,t-1}$) and carbon dioxide ($CO_{2,t-1}$) of the previous summer. Model M3 is model M2 augmented by the stem circumference (S_{cir}).

2.8. Quantile regression

Due to the reduced but still existent genetic variability and the wide

geographic distribution of the analyzed downy birch trees, we also employed quantile regression (for introductions and reviews see Koenker and Hallock, 2001; Cade and Noon, 2003; Koenker, 2017; for an extensive treatment, see Koenker, 2005). Quantile regression is a distribution-free method, where the quantiles of the response distribution are modeled directly (Koenker, 2005). The approach allows the coefficient estimates of the different explanatory variables to vary across the conditional response distribution, which alleviates the problem of model misspecification (Cade and Noon, 2003). Similar to mean regression, a model structure of the form (1) is assumed, but instead of the conditional expectation (2), the conditional quantile

$$Q_{(Y|\mathbf{X})} (\tau) = X_1 \beta_{1\tau} + \ldots + X_P \beta_{P\tau} \tag{3}$$

is modeled. In (3), $Q_{(Y|\mathbf{X})} (\tau)$ denotes the conditional τ-quantile of the response variable Y given the explanatory variables $\mathbf{X}$ and the coefficients of (3) may vary across the different conditional quantiles. Identification of the conditional τ-quantile requires that $Q_{(U|\mathbf{X})} (\tau) = 0$ (Koenker, 2005). In quantile regression, coefficient estimates result from minimizing the absolute sum of errors through linear programming (Portnoy and Koenker, 1997; Koenker and Hallock, 2001). For all plots of the quantile effects, heteroscedasticity robust standard errors proposed by Powell (1991), were used.

All statistical analyses were carried out in R version 4.3.2 (R Core Team, 2022) using the package quantreg (Koenker et al., 2023). The visualization in the paper were created using the packages cowplot (Wilke, 2024), gridExtra (Auguie and Antonov, 2017), ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2023), ggspatial (Dunnington et al., 2023) and RColorBrewer (Neuwirth, 2022).

3. Results

3.1. Pollen, flower and catkin production

Pollen production per catkin (P_{ca}) for all selected birch trees in the IPGs across Europe was 1.92 ± 1.29 million pollen grains in 2019, 2.07 ± 1.42 million pollen grains in 2020 and 2.53 ± 1.53 million pollen grains in 2021 (see Table 2). P_{ca} of individual trees varied within a wide range from 227,625 (minimum in 2021) to 7 million pollen grains (maximum in 2019). In 2021, mean P_{ca} was 22% higher compared to 2020 and 32% higher compared to 2019. In addition, the mean pollen production per flower (P_{fl}) and per volume unit of crown (P_{vuc}) in 2021 were higher compared to both 2019 and 2020. Specifically, P_{fl} in 2021 showed a 35% increase compared to 2019 and a 37% increase compared to 2020. Similarly, P_{vuc} in 2021 exhibited a 64% increase against 2019 and an increase by 8% compared to 2020 (Table 2).

For other flower and catkin metrics, their maxima were mostly registered in 2020. The number of flowers per catkin (Fl_{ca}) ranged between 65 and 145 with an average of 113 in 2019, 117 in 2020 and 107 in 2021. The number of catkins in a crown sampling unit (C_{su}; 0.125 m^3) ranged between 5 and 100 with an average of 30 in 2019, 40 in 2020 and 32 in 2021.

Table 2 shows that the null hypothesis of the Kruskal Wallis test was never rejected at a significance level of α = 0.05. According to the test results, there were no indications that the samples of reproductive metrics were generated by different distributions across years. For flowers per catkin (Fl_{ca}), it was marginally significant (p = 0.069). Fig. 2 suggests that the underlying distribution was non-normal and that there were potential outliers in the pollen production metrics. These were indicated by the observations exceeding or falling below the whiskers of the boxplots, where the maximum length or the whiskers is 1.5 times the interquartile range (dots in Fig. 2).

3.2. Geographic distribution of pollen production

Fig. 3 displays the geographic distribution of P_{ca} at the selected IPGs

Table 2

Descriptive statistics of pollen, flower and catkin production: Pollen production per flower (P_{fl}), catkin (P_{ca}) and volume unit of crown (P_{vuc}); flower production per catkin (Fl_{ca}) and volume unit of crown (Fl_{vuc}), and catkin production per crown sampling unit (C_{su}; 0.125 m^3) and volume unit of crown (C_{vuc}) for the IPG birch trees across Europe during 2019–2021. Kruskal Wallis test (p-value) indicating that the central tendency of the distribution of the variables is identical across the years 2019–2021.

| Reproductive metric	Year	Minimum	Maximum	Mean	Median	Standard deviation	Kruskal Wallis (p-value)
Pollen production							
P_{fl}	2019	3926	58,458	17,602	13,908	11,700	0.123
	2020	3172	43,085	17,333	14,489	10,861	
	2021	1711	47,692	23,715	24,160	13,936	
P_{ca}	2019	413,000	7,029,625	1,918,125	1,597,407	1,286,134	0.229
	2020	290,250	6,118,000	2,074,821	1,828,500	1,420,317	
	2021	227,625	5,580,000	2,526,685	2,271,000	1,530,021	
P_{vuc}	2019	21,648,000	1,730,560,000	495,982,353	431,818,000	441,787,251	0.568
	2020	21,670,000	4,032,800,000	754,305,379	446,964,000	913,352,274	
	2021	13,476,000	4,464,000,000	813,038,640	399,452,000	1,000,533,451	
Flower production							
Fl_{ca}	2019	79	145	113	113	14	0.069
	2020	91	142	117	118	14	
	2021	65	133	107	109	15	
Fl_{vuc}	2019	4512	76,560	28,525	24,240	19,211	0.185
	2020	5080	106,400	38,072	34,080	24,979	
	2021	4464	93,600	28,974	26,600	22,195	
Catkin production							
C_{su}	2019	5	66	30	30	19	0.286
	2020	5	100	40	38	24	
	2021	6	100	32	30	23	
C_{vuc}	2019	40	528	244	240	150	0.286
	2020	40	800	318	304	193	
	2021	48	800	258	240	187	
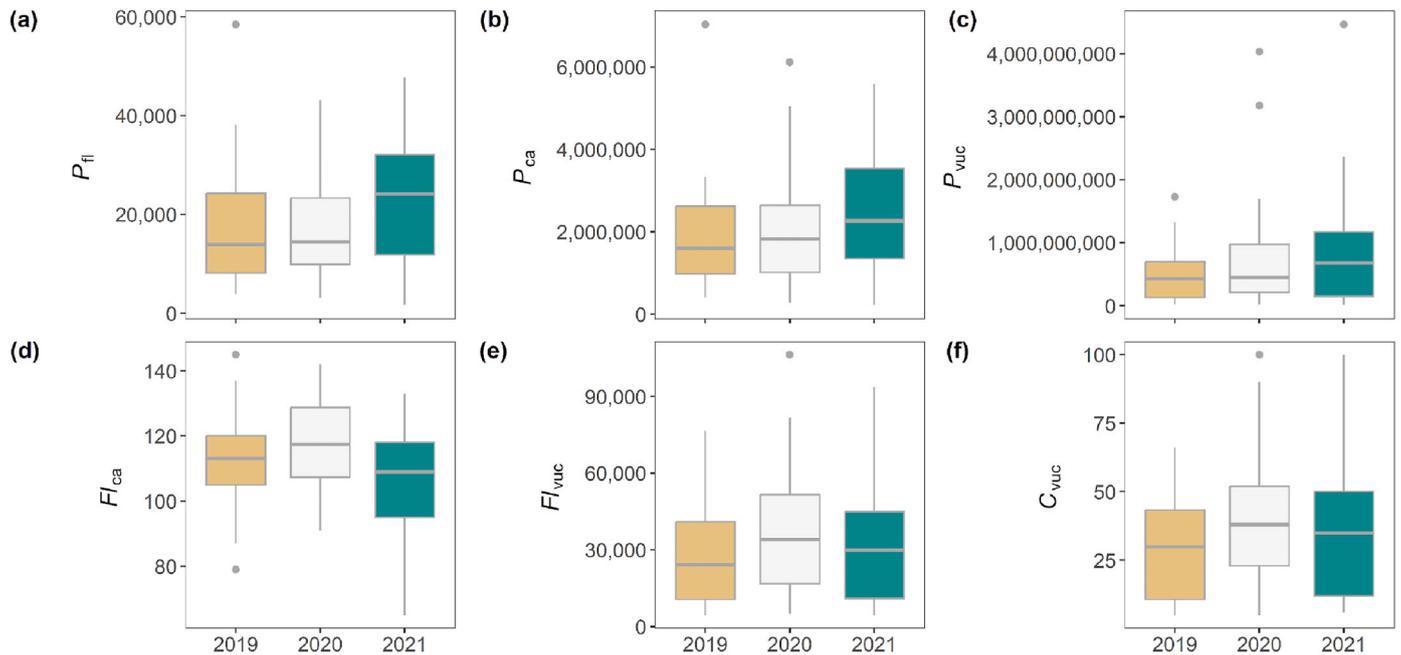
Fig. 2. Boxplots of pollen production per (a) flower (P_{fl}), (b) catkin (P_{ca}) and (c) volume unit of crown (P_{vuc}); flower production per (d) catkin (Fl_{ca}) and (e) volume unit of crown (Fl_{vuc}), and (f) catkin production per volume unit of crown (C_{vuc}) (ordinate) estimated for selected IPG birches across Europe during 2019–2021 (abscissa). Interquartile range (IQR) represented by height of boxes, median by bold horizontal lines, upper (lower) whiskers indicate minimum of maximum (minimum) of metric and 1.5 times IQR, dots represent observations exceeding or falling below 1.5 times IQR.

for the three years. In 2019, the highest P_{ca} was estimated for Waldfeucht (approx. 7 million pollen grains per catkin; marked by the triangle across the three panels). For this IPG tree, the P_{ca} estimates showed a notable decline, with a decrease of 69% in 2020 and 47% in 2021 compared to 2019. As an example, the neighbouring station Kleve (marked by the diamond), located 78 km away from Waldfeucht, was found to have the highest P_{ca} in 2021 (ca. 5 million pollen grains per

catkin). This represents a substantial increase of 160% compared to the P_{ca} value in 2020, and an 83% increase compared to the P_{ca} value observed in 2019 for the same tree. Similarly, a distinct pattern was observed for the two nearest stations (within 7.2 km), Freyung-Schönbrunn and Freyung-Waldhäuser (marked by the overlapped cross signs). Freyung-Schönbrunn revealed its highest P_{ca} (ca. 2 million) in 2021 (0.45 million in 2019 and 0.5 million in 2020), while Freyung-
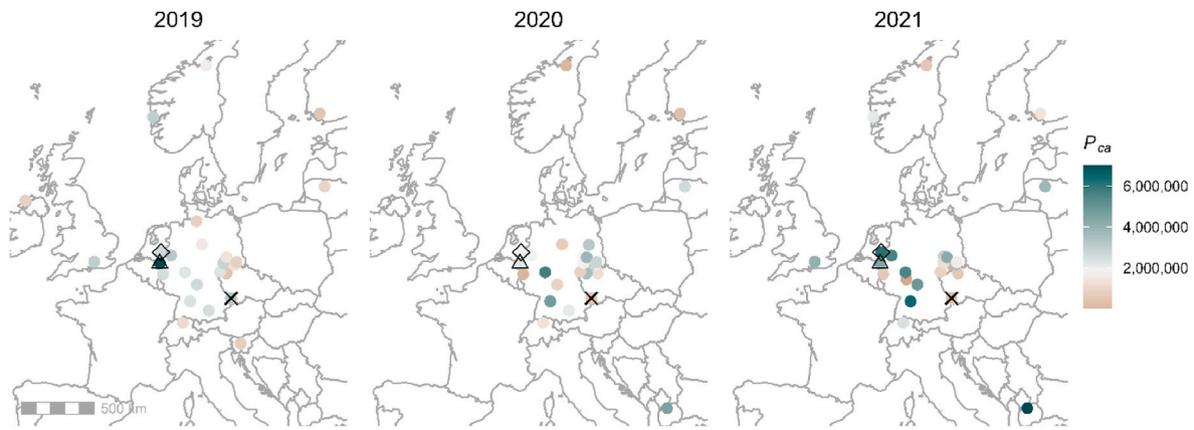
Fig. 3. Geographic distribution of P$_{ca}$ across IPG birches from 2019 to 2022. Color scheme reflects pollen production (brown for low levels, grey for average levels and dark green for high levels). Triangle: Waldfeucht, diamond: Kleve, and crosses (overlapped): Freyung-Schönbrunn and Freyung-Waldhäuser.

Waldhäuser had the highest P$_{ca}$ (ca. 3 million) in 2019 (0.73 million in 2020 and 0.68 million in 2021). This illustrates the high variability in pollen production across both space and time.

3.3. Tree-wise temporal patterns

Fig. 4 shows the temporal pattern of P$_{ca}$ and of C$_{su}$ from 2019 to 2021 for those 20 trees, which were sampled in every study year. Trees with highest P$_{ca}$ values in 2019 (i.e., group 1, N = 6) had on average 68% less pollen in the following year (min = 37%; max = 89%) and 52% less pollen in the second following year (min = 18%; max = 79%). For those trees that had the maximum P$_{ca}$ in 2020 (i.e., group 2, N = 4), we found that P$_{ca}$ was reduced by on average 51% in the preceding year (min = 34%; max = 70%) and 44% in the following year (min = 11%; max = 83%). The birches that were linked to the highest pollen production in

Fig. 4. Pollen production per catkin (P$_{ca}$) (ordinate of top display) and catkin production per sampling unit (C$_{su}$) (ordinate of bottom display) in 2019–2021 (abscissa) assessed for the trees sampled in all years at IPG stations and categorized in three groups with similar temporal behavior.

2021 (i.e., group 3, N = 10) had on average 41% less pollen in 2020 and 55% less pollen in 2019.

Regarding C$_{su}$, trees with the highest C$_{su}$ values in 2019 (group 1, N = 7) were found with an average reduction of 35% in catkins in 2020 (min = 0%; max = 80%) and 2021 (min = 8%; max = 80%). Trees with C$_{su}$ maximum in 2020 (Group 2, N = 10) were estimated with an average decline of 55% in catkins in the preceding year (min = 10%; max = 84%) and a 56% reduction in the following year (ranging from 25% to 90%). Birch trees associated with the highest catkin production in 2021 (group 3, N = 3) displayed an average reduction of 16% in 2020 and 64% in 2019.

3.4. Mean regression

In the following subsection, the results of regressions of the pollen production metrics P$_{ca}$, C$_{su}$ and P$_{vuc}$ are summarized. Note that all statements made about the effects of the explanatory variables on the response hold on average and ceteris paribus. For P$_{ca}$, specification M1, which includes only meteorological variables of the previous summer, singled out mean temperature as the most important explanatory variable (p = 0.005). The effect of temperature was found to be positive, suggesting that, P$_{ca}$ increases with increasing temperature. Adding atmospheric gas variables in specification M2 showed that O$_{3,t-1}$ (in addition to Tavg$_{t-1}$) was different from zero (p = 0.013). The effect was found to be negative, which indicates that P$_{ca}$ decreases with increasing levels of ozone. The highest adjusted R^2 (18.2%) resulted for specification M3 when also taking the stem circumference into account.

For C$_{su}$, the model based solely on meteorological variables (M1) had the lowest adjusted R^2 (6.8%), while the two explanatory variables included in the model, Tavg$_{t-1}$ and PPsum$_{t-1}$, were shown to exert a positive effect on the response (p = 0.029, p = 0.009). Adding atmospheric gas concentration variables (M2) resulted in an improvement in the model fit (adj. R^2 = 11.3%), maintaining qualitatively identical conclusions for the meteorological variables temperature (p = 0.009) and precipitation (p = 0.040). Additionally, a negative effect of O$_{3,t-1}$ (p = 0.02) on C$_{su}$ was observed in the model. This also holds true for specification M3, which adds the further explanatory variable stem circumference. For this model, the adjusted R^2 (10.6%) decreased compared to specification M2.

When considering P$_{vuc}$ as the response, the lowest adjusted R^2 was found when only accounting for meteorological variables (6.7%). R^2 was highest for specification M2, in which meteorological and pollutant concentration variables were included (17.1%). Similar to the results found for C$_{su}$, specification M3 was associated with a lower adjusted R^2 (16.2%) compared to M2.

In summary, the mean regression results indicate that the preceding summers' mean temperature and O$_3$ concentration levels are most
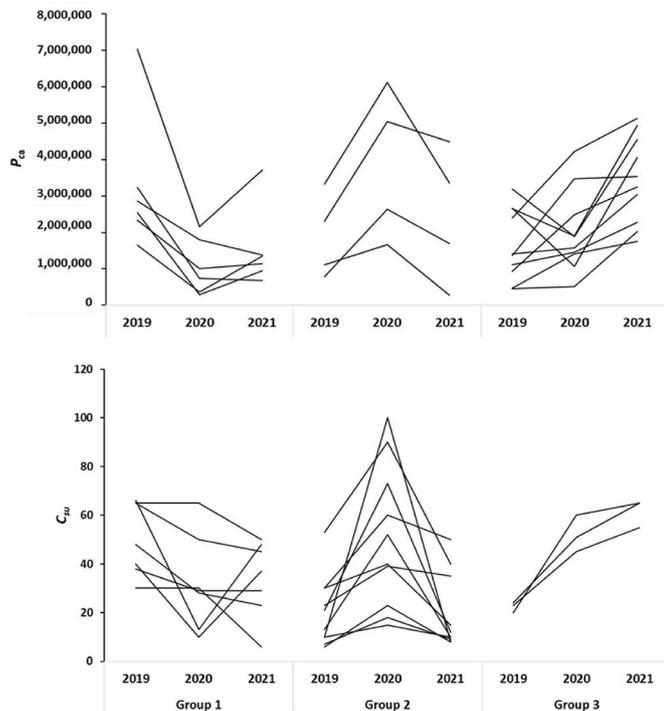
important in the production of pollen per catkin (P_{ca}). Our results suggest that elevated $Tavg_{t-1}$ corresponds to an increase in P_{ca}, while an increase in $O_{3,t-1}$ has the opposite effect. Catkin quantities, on the other hand, are influenced by temperature, precipitation, and O_3 concentration levels of the preceding summer. Higher values in these meteorological variables lead to increased catkin production (C_{su}), while an elevated $O_{3,t-1}$ is associated with decreased C_{su}. Pollen production at the larger scale (at the level of the volume of the crown) is therefore also mostly influenced by temperature and ozone.

Among the considered specifications, M2 has the lowest AIC values (see Table 3) across all three dependent variables. We focus on this model variant in the following and describe the results for P_{ca}.

3.5. Quantile regression

The documented non-normality in the pollen production metrics (see Table 2 and Fig. 2; Shapiro-Wilk tests rejected the null of normality for all three metrics with p-values <0.001), and the presence of genetic variability and potential outliers may render the linear regression results and their interpretations unreliable due to specification bias and/or inconsistent standard error estimates. We therefore chose quantile regression as modeling alternative.

In the following, we describe the quantile regression results for specification M2. Fig. 5 summarizes the results via quantile plots, which show the coefficient estimates across the conditional τ-quantiles of the response distribution separately for each explanatory variable. The plots indicate the coefficient estimates together with the 90%-confidence region, which is illustrated by the shaded area. The considered quantiles range from $\tau = 0.2$ to $\tau = 0.8$. Via the horizontal lines, the plots also include the mean regression results (dotted line) and the corresponding 90% confidence region (dashed lines) for reference.

Fig. 5 illustrates the presence of mild quantile effects across the conditional response distribution. For $Tavg_{t-1}$, for example, the effect of the variable on the response – when conditioning for all other explanatory variables – increases across τ for all considered quantiles. The effect is indistinguishable from zero for $\tau = 0.2$ at a significance level of $\alpha = 0.1$ and positive for $\tau \in (0.3, 0.8)$. This implies that the mean temperature of the previous summer exerts a positive effect on pollen production for all trees, except the ones with the lowest pollen production levels. For $O_{3,t-1}$, similar statements hold, but here, the effects of the variable on the response are zero for $\tau < 0.5$ and negative for all other values of τ. This suggests that the effects of $O_{3,t-1}$ on pollen production is negative for the trees with a pollen production equal to or higher than the median level. For $PPsum_{t-1}$ and $CO_{2,t-1}$, the effects are indistinguishable from zero for all quantiles. The centercept can be considered as a prediction of the τ-quantile of pollen production for the IPG trees with the explanatory variables set to their respective medians (see Appendix Table 2 which summarizes the descriptive statistics for the meteorological variables). Note that when considering the mean regression effects only, similar conclusions result for variables $PPsum_{t-1}$

and $CO_{2,t-1}$. For $Tavg_{t-1}$ and $O_{3,t-1}$, however, the (global) positive and negative effects indicated by the mean regression results may be an oversimplification.

For C_{su}, the effects of $Tavg_{t-1}$ are positive for $\tau > 0.7$. The effect of $O_{3,t-1}$ is negative for $\tau > 0.5$, while for $PPsum_{t-1}$, the effects are indistinguishable from zero for all quantiles (see Appendix Fig. 1). For P_{vuc}, the effects of $Tavg_{t-1}$ are positive for $\tau > 0.7$ and negative for O_3 concentrations when $\tau > 0.5$ (see Appendix Fig. 2).

4. Discussion

4.1. Pollen, flower and catkin production

This study investigated the reproductive metrics of downy birch trees from IPGs across Europe along spatial gradients over a period of three years. We measured the mean pollen production of catkins (P_{ca}) in the range of 1.9 million to 2.5 million. These measures are an important estimation range when representing pollen production of downy birch across its distribution range. However, this estimate was even higher (between 2.5 million to 5 million) when studied along an altitudinal gradient in the European Alps (Ranpal et al., 2023). In the contemporary study years, pollen production estimations of *Betula pendula* (silver birch) with comparable sample sizes and methods were estimated with <1 million (Kolek, 2021), <1.6 million (Jetschni et al., 2023) and up to 1.7 million (Ranpal et al., 2022). Based on these estimates, we suggest that *B. pendula* produce less P_{ca} as compared to *B. pubescens*.

4.2. Year-to-year variation in pollen production

Based on mean values of all selected IPGs across Europe, our analysis revealed the lowest means for P_{ca} in 2019 and the highest in 2021. This year-to-year variation, however, was not significant in all the studied reproductive metrics of pollen, flowers, and catkins. However, substantial differences between single sites across the years get obvious, as discussed for Fig. 3. At a small geographical scale, Ranpal et al. (2022, 2023) also found annual variations in pollen production during the studied years.

Masting can play a substantial role in influencing reproductive metrics as it can mask the influences of environmental stressors, for example, temperature (Ranpal et al., 2023). Masting can either be limited to the population level (Ranta et al., 2005) or can be observed simultaneously in larger regions (Ranta et al., 2008) as well as continents (Bogdziewicz et al., 2021). In our study, maximum values of P_{ca} or C_{su} were not simultaneously observed for all trees in one specific year. For most of the trees (N = 10), maximum P_{ca} values were obtained in 2021; regarding C_{su}, most trees (N = 10) produced the highest catkin numbers in 2020. These findings suggest that the observed year-to-year variations in pollen and catkin production are not solely driven by genetic factors, as each group of trees categorized in Fig. 4 comprises individuals of different genotypes. As the difference in P_{ca} and C_{su} between

Table 3

Mean regression models according to the specifications given in Table 1. Columns detail explanatory variables, residual standard error, degrees of freedom, adjusted R^2, p-value of overall F-test that all coefficients are jointly zero, Akaike information criterion (AIC).

| Model	Explanatory variables (° p < 0.1, *p < 0.05, **p < 0.01, ***p < 0.001)	Residual standard error	Degrees of freedom	Adjusted R^2	p-value	AIC
P_{ca}						
M1	$Tavg_{t-1}$**, $PPsum_{t-1}$	1,367,000	90	0.089	0.015	2896.702
M2	$Tavg_{t-1}$***, $PPsum_{t-1}$, $O_{3,t-1}$*, $CO_{2,t-1}$°	1,288,000	88	0.174	0.0003	2887.490
M3	$Tavg_{t-1}$**, $PPsum_{t-1}$, $O_{3,t-1}$*, $CO_{2,t-1}$°, $S_{cir,t}$	1,281,000	87	0.182	0.0004	2887.529
C_{su}						
M1	$Tavg_{t-1}$*, $PPsum_{t-1}$**	22.40	89	0.068	0.016	838.129
M2	$Tavg_{t-1}$**, $PPsum_{t-1}$*, $O_{3,t-1}$*, $CO_{2,t-1}$	21.86	87	0.113	0.006	835.537
M3	$Tavg_{t-1}$**, $PPsum_{t-1}$*, $O_{3,t-1}$*, $CO_{2,t-1}$, $S_{cir,t}$	21.95	86	0.106	0.012	837.201
P_{vuc}						
M1	$Tavg_{t-1}$**, $PPsum_{t-1}$°	766,900,000	89	0.067	0.017	4030.291
M2	$Tavg_{t-1}$***, $PPsum_{t-1}$, $O_{3,t-1}$**, $CO_{2,t-1}$	722,900,000	87	0.171	0.0004	4021.32
M3	$Tavg_{t-1}$***, $PPsum_{t-1}$, $O_{3,t-1}$**, $CO_{2,t-1}$, $S_{cir,t}$	726,700,000	86	0.162	0.001	4023.225
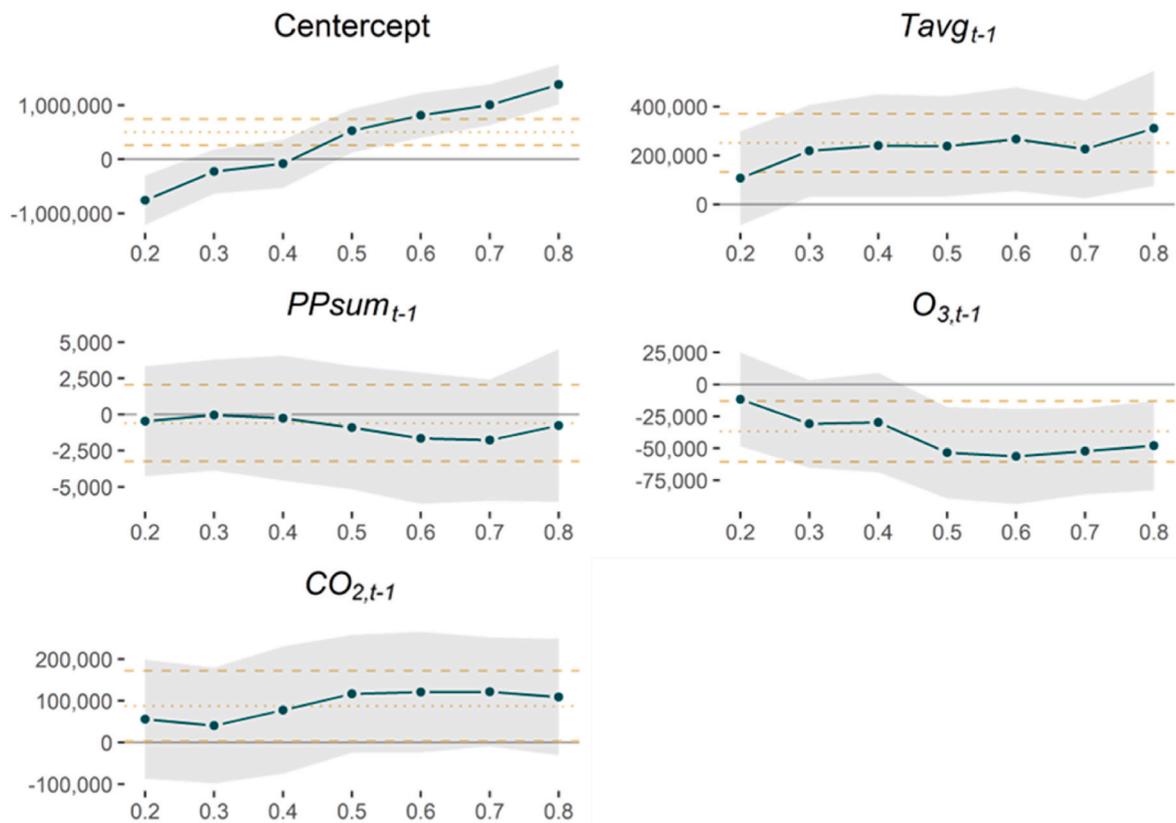
Fig. 5. Quantile plots for specification M2; effects of environmental variables (ordinate) on P_{ca} across conditional response distribution for τ-quantiles, $\tau \in (0.2, 0.8)$ (abscissa) shown via points. Shaded area represents 90%-confidence region. Horizontal lines indicate mean regression effect (dotted) and corresponding 90%-confidence region (dashed).

the years before and after the registered maxima were quite large, longer time-series are needed to identify and analyze masting events in more detail.

4.3. Effects of environmental variables on pollen production

The understanding of environmental determinants of pollen production is crucial for investigating trends in the face of future climate change. In this study, we assessed the influences of different environmental variables on birch pollen production, while also controlling for stem circumference (in one model specification).

Our models that combine atmospheric gases and meteorological data appeared most appropriate for modeling the pollen production metrics. We found that temperature of the previous summer had positive effects on both, pollen production and catkin formation, while precipitation increased the number of catkins. In contrast, O_3 concentrations had a negative effect on pollen and catkin production. The relationship between temperature and pollen production found in this study are in line with the findings of previous studies (Damialis et al., 2011; Ranpal et al., 2023). We had previously reported that a higher pollen production of downy birch during a non-masting year was associated with higher temperature of the preceding summer in birch trees along an altitudinal gradient (Ranpal et al., 2023). Investigations on other species, such as the herbaceous common ragweed (*Ambrosia artemisiifolia*), have demonstrated that increases in temperature were associated with a higher pollen production (Ziska et al., 2003). However, our findings are in contrast with the results of Jochner et al. (2013) and Jetschni et al. (2023), who observed a notable decrease in pollen production per catkin in silver birch within urban areas (associated with elevated temperatures and higher pollutant concentrations). Our study indicates that birch trees could modulate their physiological processes to optimize

pollen production under varying temperature regimes. Especially those trees which were characterized by high pollen production levels were associated with increases of P_{ca} under high mean temperature of the previous summer. It may be possible that birch trees show an initial boost in pollen production as temperatures rise, but there could be a threshold beyond which further temperature increases might hinder their physiological performance. Our findings could be interpreted such that the examined temperature range is still within the realm of positive impact on reproduction.

Plant biomass of Scots pine individuals have been reported to be adversely affected by elevated O_3 in fumigation experiments (Manninen et al., 2009). However, knowledge on the effect of O_3 on pollen production of birch is largely lacking. Our study has revealed that O_3 has adverse effects on both pollen and catkin production, and these effects vary across different parts of the conditional distribution of the reproductive metrics. Quantile regressions revealed that the effect of O_3 on P_{ca} was negative for quantiles $\tau \geq 0.5$ (Fig. 5), while being indistinguishable from zero for $\tau < 0.5$. Similarly, in the case of C_{su} and P_{vuc}, O_3 exerted a negative effect for $\tau \geq 0.6$ (see Appendix Figs. 1 and 2). Regarding reproductive outputs, Darbah et al. (2008) found reduced seed mass and germination rates of *Betula papyrifera* under the elevated O_3 condition. In another study, Ziska (2002) did not find any significant difference in floral biomass of ragweed under elevated O_3 concentrations. O_3 is a gaseous pollutant that enters plants via the stomata. High levels of O_3 can lead to oxidative stress in plants and can disrupt photosynthesis (Gandin et al., 2021) which could potentially also limit pollen production. Further studies, e.g., based on experimental approaches, are needed to investigate the role of O_3 on reproduction of downy birch in more detail.

Rising levels of CO_2 in the atmosphere can fertilize vegetation (Kudeyarov et al., 2006), increase the ability of plants to

photosynthesize (Drake et al., 1997) and was found to induce higher pollen production in some plants such as ragweed (Rauer et al., 2021; Rogers et al., 2006; Ziska and Caulfield, 2000) and timothy grass (Albertine et al., 2014) as well as in trees, such as pine (Ladeau and Clark, 2006) and oak (Kim et al., 2018; Ladeau and Clark, 2006). As we do not have a longer time-series and therefore cannot cover a period with a large increase in CO_2, we can only relate the regional differences (range: 8 ppm) of CO_2 based on a coarse resolution ($0.75° \times 0.75°$) to pollen production. In this case, our result only revealed an association between elevated CO_2 and P_{ca} at marginal significance.

The observation of quantile effects in this study offers novel insights into the relationship between environment and pollen production. Our results indicate that the effects of mean temperature and O_3 in the previous summer vary across the conditional response distribution. While the effects of temperature are zero for trees with low levels of pollen production and positive for trees with high levels of pollen production, the effects of O_3 are zero for trees with low pollen production and negative for trees with pollen production levels above the conditional median. The large confidence regions in our analysis emphasizes the importance of expanding the sample sizes in future studies to enhance the reliability of the conclusions. Overall, our results highlight the benefits of expanding the analysis of pollen production metrics beyond the conditional mean.

The study's geographic scope is constrained by the uneven distribution of the IPGs across Europe, limiting the representation of birches in certain regions. Additionally, the similar environmental conditions within each IPG site restrict the variation in the explanatory variables. Future research should expand sampling beyond the IPG network to capture a more comprehensive representation of birch habitats and environmental factors influencing pollen production. Despite these limitations, the study provides valuable insights into continental-scale patterns and drivers of birch pollen production, increasing our understanding of the potential impacts of global change on this important aeroallergen.

4.4. Genetic effects

Studying IPG plants can be compared with an experimental approach since all birch individuals originate from Germany and were transferred to other sites in Europe (Renner and Chmielewski, 2021). Translocated individuals do not alter their DNA sequence to adapt to new environmental conditions (Amaral et al., 2020; Richards et al., 2017). However, small RNAs might participate in mechanisms that trigger epigenetic gene expression changes in response to environmental cues (Duempelmann et al., 2020) and such changes in small RNA components could be passed over to bud cells and therefore to the next generation (Vanden Broeck et al., 2018). Therefore, apart from environmental influences, the variations in reproductive metrics of IPG birches could be due to clonal differences and potential epigenetic effects. Although, we found differences in genetics of the IPG trees, many birches present a distinct genotype. Thus, we conclude that the variability of genetic effects is extremely reduced in this study. This assertion holds true for all studies incorporating data of the International Phenological Gardens network. Therefore, our approach can be considered a sophisticated space-for-time (SFT) approach, as the genetic variability, which often poses a disadvantage in SFT studies, is largely reduced in our study.

5. Conclusion

The present research is novel as the study site covers IPGs in a large geographical region across Europe. We did not observe any clear spatial pattern in pollen production which reflects the complex interactions between birch trees and their environment. The findings of this paper indicate that birch pollen production increases with higher mean air temperature but decreases with elevated ozone concentrations. Moreover, quantile regression enabled us to quantify the effects of the environmental variables across different pollen production levels. Future research should focus on how individuals and communities can adapt to increased pollen and allergen levels, e.g., using improved pollen forecasts or urban planning that considers allergen-free vegetation. Collaboration between climatologists, ecologists, biologists, medical researchers, public health experts, and statisticians as demonstrated by this publication is crucial to address the multifaceted nature of these challenges.

CRediT authorship contribution statement

Surendra Ranpal: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Susanne von Bargen:** Writing – review & editing. **Stefanie Gilles:** Writing – review & editing. **Daria Luschkova[3]:** Writing – review & editing. **Maria Landgraf:** Writing – review & editing. **Pawel Bogawski:** Writing – review & editing, Visualization, Methodology. **Claudia Traidl-Hoffmann:** Writing – review & editing, Funding acquisition, Conceptualization. **Carmen Büttner:** Writing – review & editing, Funding acquisition, Conceptualization. **Athanasios Damialis:** Writing – review & editing, Validation, Methodology. **Markus Fritsch:** Writing – review & editing, Visualization, Validation, Software, Methodology, Formal analysis. **Susanne Jochner-Oette:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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.

Data availability

Data will be made available on request.
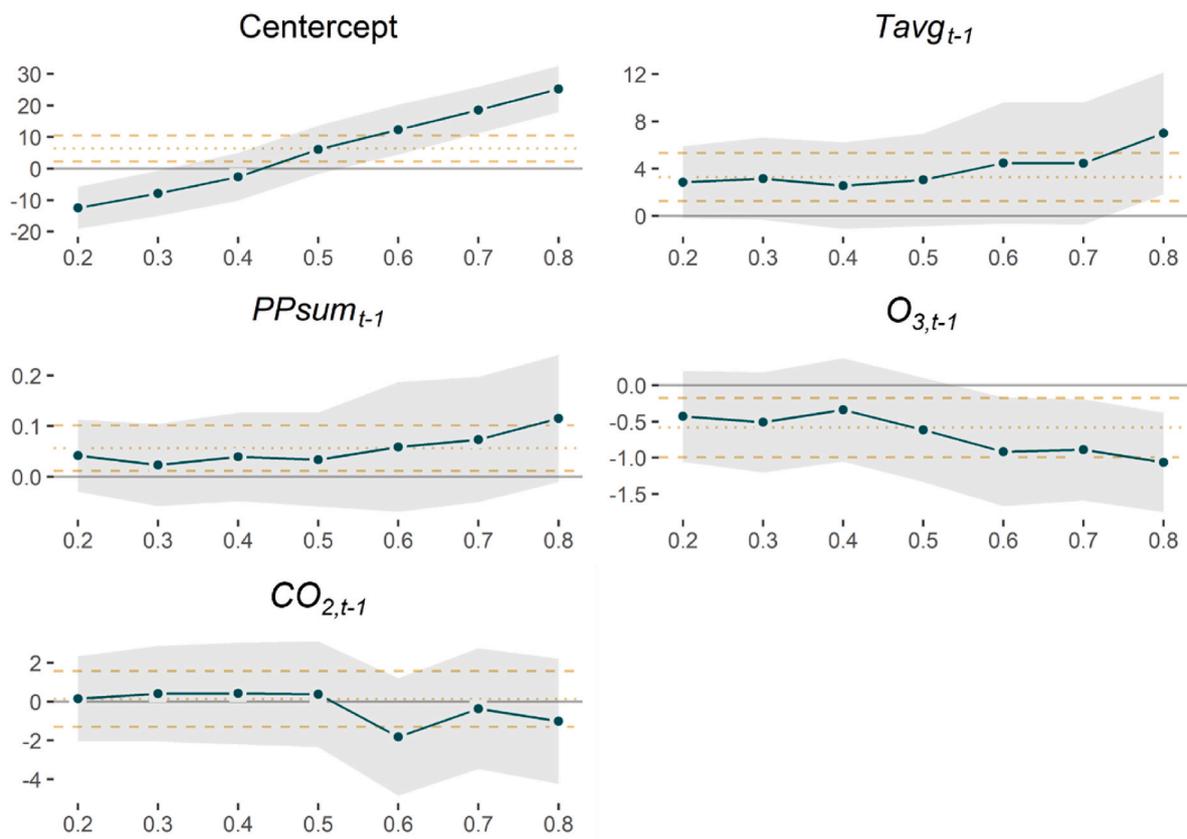
Appendix

Appendix Table 1

List of International Phenological Gardens and countries from which up to three downy birch trees were selected for this study. Years (1 = 2019, 2 = 2020 and 3 = 2021) in which samples were available; elevation (meters above sea level); triannual mean air temperature (Tavg) from 2018 to 2020 (°C) and triannual mean precipitation sum (PPsum) from 2018 to 2020 (mm).

| IPG	Site	Country	Years	Coordinates	Elevation	no. of trees	Plantation year	Tavg	PPsum
1	Trondheim	Norway	1, 2, 3	N 63° 29′ E 10° 52′	69	2	1963, 2007	5.99	978
2	Bergen-Fana	Norway	1, 3	N 60° 16′ E 5° 21′	50	2	1994, 1999	8.05	2441
8	Turku	Finland	1, 2, 3	N 60° 29′ E 22° 45′	45	2	1965	6.92	637
24	Offenbach	Germany	1, 2, 3	N 50° 05′ E 08° 46′	114	1	2012	11.76	543
27	Stuttgart-Hohenheim	Germany	1, 2, 3	N 48° 43′ E 09° 13′	380	2	1960	11.36	592
36	München-Grafrath	Germany	1, 2, 3	N 48° 08′ E 11° 09′	569	2	1996, 2009	9.75	785
38	Freyung-Schönbrunn	Germany	1, 2, 3	N 48° 52′ E 13° 31′	820	1	2012	8.35	999
40	Freyung-Waldhäuser	Germany	1, 2, 3	N 48° 55′ E 13° 27′	967	1	2005	6.70	1014
42	Tharandt-Hartha	Germany	1, 2, 3	N 50° 58′ E 13° 32′	358	2	1960, 1969	9.84	557
46	Zürich-Birmensdorf	Switzerland	1, 2, 3	N 47° 21′ E 08° 27′	544	1	1965	10.65	983
55	Ljubljana	Slovenia	1	N 46° 04′ E 14° 30′	299	3	1960,1990, 2007	12.18	1274
62	Skopje	North Macedonia	2, 3	N 42° 01′ E 21° 24′	294	1	1980	13.73	660
72	London	United Kingdom	1, 3	N 51° 12′ W 00° 46′	83	1	2005	11.47	731
77	Hamburg-Quickborn	Germany	1	N 53° 44′ E 09° 52′	13	2	1988	10.28	736
80	Thyrow	Germany	1, 2	N 52° 15′ E 09° 52′	43	1	1998	11.19	406
85	Praha-Doksany	Czech Republic	2, 3	N 50° 27′ E 14° 10′	158	1	2000	10.73	389
90	Hellenthal	Germany	1, 2, 3	N 50° 24′ E 06° 22′	686	1	2009	8.97	905
112	Glenveagh	Ireland	1	N 55° 01′ W 07° 58′	118	1	2007	9.47	1847
152	Siauliai	Lithuania	1, 2, 3	N 55° 55′ E 23° 16′	126	1	2005	8.61	510
189	Linden	Germany	1, 2, 3	N 50° 31′ E 08° 41′	171	1	2003	10.83	567
190	Graupa	Germany	1, 2, 3	N 51° 00′ E 13° 55′	181	1	2004	10.67	540
191	Heinzebank	Germany	1, 2	N 50° 41′ E 13° 08′	605	1	2005	8.67	715
192	Kretscham-Rothensehma	Germany	1, 2	N 50° 27′ E 12° 59′	852	1	2005	6.93	827
193	Doberschütz	Germany	1, 2, 3	N 51° 31′ E 12° 41′	99	1	2005	11.25	443
194	Eich	Germany	1, 2, 3	N 50° 33′ E 12° 20′	449	1	2005	9.61	634
195	Leipzig	Germany	1, 2, 3	N 51° 07′ E 12° 41′	201	1	2009	10.99	495
196	Taura	Germany	1, 2, 3	N 51° 28′ E 13° 00′	127	1	2005	10.96	428
210	Sarajevo	Bosnia and Herzegovina	1, 2, 3	N 43° 52′ E 18° 25′	633	1	2013	9.72	899
212	Mostar	Bosnia and Herzegovina	1	N 43° 20′ E 17° 47′	98	1	2014	14.09	1158
220	Würzburg	Germany	1, 2, 3	N 49° 45′ E 09° 56′	193	1	2010	11.37	476
221	Roßla	Germany	1, 2, 3	N 51° 27′ E 11° 04′	148	1	2011	10.35	452
224	Kleve	Germany	1, 2, 3	N 51° 47′ E 06° 10′	13	1	2009	11.46	682
226	Essen	Germany	1, 2, 3	N 51° 24′ E 06° 57′	155	1	2008	11.93	723
227	Recklinghausen	Germany	1, 2, 3	N 51° 35′ E 07° 13′	54	1	2009	11.53	695
228	Ohorn	Germany	1, 2, 3	N 51° 10′ E 14° 02′	306	1	2011	10.34	556
230	Waldfeucht	Germany	1, 2, 3	N 51° 05′ E 06° 03′	30	1	2011	11.74	625
231	Braunschweig	Germany	1, 2	N 52° 17′ E 10° 26′	82	1	2011	11.19	493

Appendix Table 2

Descriptive statistics for the meteorological variables for IPG sites included in this study analysis and Kruskal Wallis test (p-value) indicating that the central tendency of the distribution of the variables is identical across years 2019–2021.

Meteorological variables	Description	Year	Minimum	Maximum	Mean	Median	Standard deviation	Kruskal Wallis (p-value)
$Tmin_{t-1}$	Minimum temperature (°C) of the preceding summer	2018	1.5	8.1	5.4	5.5	1.6	0.597 (0.742)
		2019	1.8	7.7	5.2	5.6	1.5	
		2020	2.6	7.8	5.5	5.8	1.4	
$Tavg_{t-1}$	Average temperature (°C) of the preceding summer	2018	5.7	12.3	10	10.5	1.8	0.386 (0.825)
		2019	5.5	13.9	9.9	10.5	1.9	
		2020	6.6	13.4	10.1	10.6	1.8	
$Tmax_{t-1}$	Maximum temperature (°C) of the preceding summer	2018	10.1	17.3	14.,6	15.1	2.3	0.401 (0.818)
		2019	9.6	19.8	14.5	15.1	2.3	
		2020	10.7	19.1	14.5	15.5	2.4	
$PPsum_{t-1}$	Total precipitation (mm) of the preceding summer	2018	329	2102	757	590	461	2.58 (0.276)
		2019	427	1054	692	683	182	
		2020	411	2945	856	684	608	
RH_{t-1}	Relative humidity (%) of the preceding summer	2018	70.3	84.3	76.3	75.7	4	0.333 (0.847)
		2019	70.7	82.,9	76.2	75.3	3.2	
		2020	70.5	87.1	76.4	75	4.6	
GR_{t-1}	Global solar radiation (W/m²) of the preceding summer	2018	35468	54538	48023	49296	5131	31.722 (0.000)
		2019	29649	60432	38329	37069	6110	
		2020	34382	55748	46399	47530	5937	

Appendix Fig. 1. Quantile plots for specification M2; effects of environmental variables (ordinate) on C_{su} across conditional response distribution for τ-quantiles, $\tau \in$ (0.2, 0.8) (abscissa) shown via points. Shaded area represents 90%-confidence region. Horizontal lines indicate mean regression effect (dotted) and corresponding 90%-confidence region (dashed).
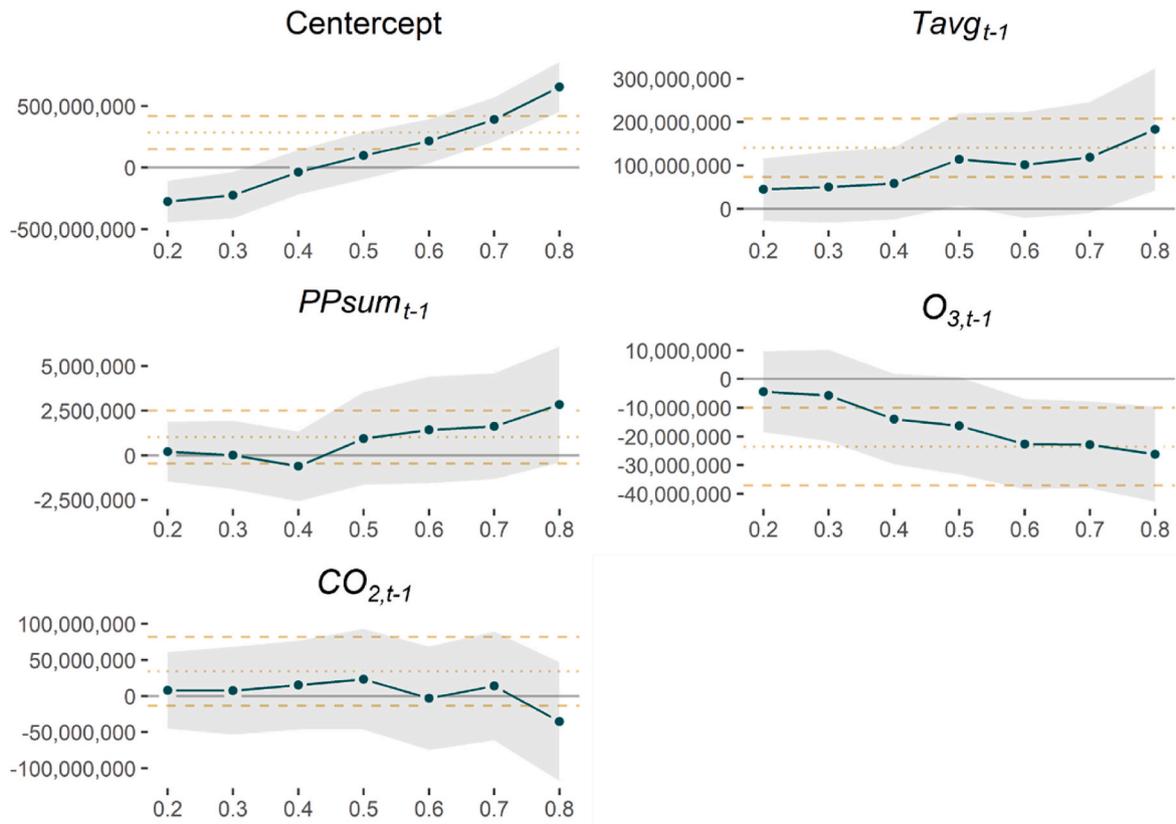
Appendix Fig. 2. Quantile plots for specification M2; effects of environmental variables (ordinate) on P_{vuc} across conditional response distribution for τ-quantiles, τ ϵ (0.2, 0.8) (abscissa) shown via points. Shaded area represents 90%-confidence region. Horizontal lines indicate mean regression effect (dotted) and corresponding 90%-confidence region (dashed).

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