















Effects of future climate change on birch abundance and their pollen load

Jesús Rojo, Jose Oteros, Antonio Picornell, José M. Maya Manzano, Athanasios Damialis, Katrin Zink, Matthias Werchan, Barbora Werchan, Matt Smith, Annette Menzel, Sabine Timpf, Claudia Traidl-Hoffmann, Karl Christian Bergmann, Carsten B. Schmidt Weber, Jeroen Buters

Angaben zur Veröffentlichung / Publication details:

Rojo, Jesús, Jose Oteros, Antonio Picornell, José M. Maya Manzano, Athanasios Damialis, Katrin Zink, Matthias Werchan, et al. 2021. "Effects of future climate change on birch abundance and their pollen load." *Global Change Biology* 27 (22): 5934–49.
<https://doi.org/10.1111/gcb.15824>.

Effects of future climate change on birch abundance and their pollen load

Jesús Rojo^{1,2}  | Jose Oteros³  | Antonio Picornell⁴  | José M. Maya-Manzano¹  | Athanasios Damialis^{5,6,7}  | Katrin Zink⁸ | Matthias Werchan⁹  | Barbora Werchan⁹  | Matt Smith¹⁰  | Annette Menzel¹¹  | Sabine Timpf¹²  | Claudia Traidl-Hoffmann^{6,7}  | Karl-Christian Bergmann¹³  | Carsten B. Schmidt-Weber¹  | Jeroen Buters¹ 

¹Center of Allergy & Environment (ZAUM), Member of the German Center for Lung Research (DZL), Technische Universität München/Helmholtz Center Munich, Munich, Germany

²Department of Pharmacology, Pharmacognosy and Botany, Complutense University of Madrid, Madrid, Spain

³Department of Botany, Ecology and Plant Physiology, University of Cordoba, Cordoba, Spain

⁴Department of Botany and Plant Physiology, University of Malaga, Malaga, Spain

⁵Department of Ecology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece

⁶Department of Environmental Medicine, University of Augsburg, Augsburg, Germany

⁷Helmholtz Center Munich – German Research Center for Environmental Health, Augsburg, Germany

⁸Bayerisches Landesamt für Umwelt, Schwerpunkt Klima und Energie, Referat KLIZ: Klima-Zentrum, Hof/Saale, Germany

⁹German Pollen Information Service Foundation (PID), Berlin, Germany

¹⁰School of Science and the Environment, University of Worcester, Worcester, UK

¹¹School of Life Sciences, Technische Universität München, Freising, Germany

¹²Institute of Geography, Geoinformatics Group, University of Augsburg, Augsburg, Germany

¹³Charité – Universitätsmedizin Berlin, Corporate Member of Freie Universität Berlin, Humboldt-Universität zu Berlin, Berlin Institute of Health, Berlin, Germany

Correspondence

Jesús Rojo, ZAUM-Technical University Munich, Biedersteinerstrasse 29, 80802 Munich, Germany.
Email: jesrojo@ucm.es

Funding information

This study was funded by the Bavarian State Ministry of the Environment and Consumer Protection as project K3-8503-PN-18-26-D27432/2018 and the projects TKP01KPB-73815 and TKP01KPB-73813; and by the Bavarian State Ministry of Health and Care project AP-2460-ePIN-V11-U1-D44520/2018.

Abstract

Climate change impacts on the structure and function of ecosystems will worsen public health issues like allergic diseases. Birch trees (*Betula* spp.) are important sources of aeroallergens in Central and Northern Europe. Birches are vulnerable to climate change as these trees are sensitive to increased temperatures and summer droughts. This study aims to examine the effect of climate change on airborne birch pollen concentrations in Central Europe using Bavaria in Southern Germany as a case study. Pollen data from 28 monitoring stations in Bavaria were used in this study, with time series of up to 30 years long. An integrative approach was used to model airborne birch pollen concentrations taking into account drivers influencing birch tree abundance and birch pollen production and projections made according to different climate change and socioeconomic scenarios. Birch tree abundance is projected to decrease in parts of Bavaria at different rates, depending on the climate scenario, particularly in current centres of the species distribution. Climate change is expected to result in initial increases in pollen load but, due to the reduction in birch trees, the amount of airborne birch pollen will decrease at lower altitudes. Conversely, higher altitude areas will experience expansions in birch tree distribution and subsequent increases

in airborne birch pollen in the future. Even considering restrictions for migration rates, increases in pollen load are likely in Southwestern areas, where positive trends have already been detected during the last three decades. Integrating models for the distribution and abundance of pollen sources and the drivers that control birch pollen production allowed us to model airborne birch pollen concentrations in the future. The magnitude of changes depends on location and climate change scenario.

KEYWORDS

Betula, climate change, ecological modelling, plant distribution, pollen exposure, pollen production, temperate trees

1 | INTRODUCTION

The effects of climate change have already been observed in many natural systems (Fu et al., 2015; Garcia et al., 2014; Rosenzweig et al., 2008; Ziska et al., 2019) and the impacts may increase dramatically in the future if mitigation objectives are not met (Fawcett et al., 2015). The impacts of global warming on public health issues like allergic diseases are often overlooked (Ziska & Beggs, 2012). Several of the temperate woody plants such as members of the Betulaceae family, for example, hazel (*Corylus* spp.), alder (*Alnus* spp.) and birch (*Betula* spp.), are wind pollinated and produce large amounts of allergenic pollen grains that are readily dispersed in the atmosphere (Smith et al., 2014). Birches are among the most allergenic and abundant pollen producing tree species in Central and Northern Europe (Biedermann et al., 2019; Buters et al., 2012; Rojo et al., 2020). As a consequence, birch pollen allergens cause approximately 14% of all sensitization in the general population of Germany (and 17% in adults; Haftenberger et al., 2013), and have a similar prevalence in other Central European countries (Biedermann et al., 2019; Schmitz et al., 2013; Verstraeten et al., 2019). Furthermore, the incidence of sensitization to birch pollen allergens has increased over recent decades (Biedermann et al., 2019).

Climate change can have important impacts on forest ecosystems, such as changes in composition, structure and ecosystem function (Morin et al., 2018; Thom et al., 2017). Many tree species may experience changes in physiological characteristics, such as increased productivity due to atmospheric CO₂ enrichment and temperature increases, provided that the environmental changes are within the optimal range for the metabolism of the plants (Kim et al., 2018; Xu et al., 2007). On the other hand, projected increases in temperature will promote changes in the competitive dominance between tree species, which will lead to transformations in the current configuration of the tree landscape (Hanewinkel et al., 2013). As a result, certain tree species that currently act as major allergen sources like birch may dwindle or disappear in some areas as their range contracts northward, although they may also expand their distribution into areas of higher elevation (Dyderski et al., 2018). Such displacements do not happen straight away, however, as there is a lag due to species plasticity favouring population persistence and dispersion capability as well as species competence limiting migration

rates (Prasad et al., 2020). Although, it has been suggested that, due to intraspecific variations, warm margin populations are the most vulnerable to climate change (Fréjaville et al., 2020). In addition, especially for pioneer species such as *Betula*, future disturbance rates may also influence their distribution (Drobyshev et al., 2014).

Environmental factors that control plant growth occur at multiple spatiotemporal scales, which makes it difficult to determine the direction and intensity of the expected changes (Garcia et al., 2014). For instance, the magnitude of airborne pollen concentrations, which is considered to be a proxy for flowering intensity in a given geographical area, is dependent on both short-term meteorological influences on reproductive biology (Rojo et al., 2015; Sofiev, 2017) and long-term bioclimatic changes that lead to vegetation displacements (Giesecke et al., 2019). Numerous statistical approaches have been developed for modelling the annual pollen integral (APIn) based on meteorological and biological parameters (Oteros et al., 2013; Ritenberga et al., 2018). Other studies have focused on the relationships between the spatial distribution of vegetation and general patterns of pollen emission (Lugonja et al., 2019; McInnes et al., 2017; Rojo et al., 2016). Vegetation types are displaced following changes in environmental gradients as a result of climate change, although these displacements occur at a lower rate than those changes influencing phenology and pollen production. Approaches in the field of ecological modelling allow plant distributions to be modelled and projections made for the future (Dyderski et al., 2018; Pecchi et al., 2020). Therefore, all drivers need to be taken into account in an integrative approach to model the reproductive cycle of a plant species (Kurganskiy et al., 2020; Verstraeten et al., 2019).

Birches occupy a broad geographical range in the Northern hemisphere (Wang et al., 2016). In Europe, the arboreal birches are silver birch (*Betula pendula* Roth) and downy birch (*Betula pubescens* Ehrh.). Both species are widely distributed in Central and Northern Europe but their distribution in Southern Europe is limited to mountainous and refuge areas as both species are very sensitive to summer droughts, especially in combination with warm temperatures (Beck et al., 2016; Dyderski et al., 2018).

These environmental limitations make birches vulnerable to climate change. Temperatures are projected to increase and there is significant agreement for warming between climate models for all emission scenarios (IPCC, 2014; Kjellström et al., 2018). On the

other hand, projections for precipitation are more uncertain with medium confidence for increases in Northern Europe and decreases in Southern Europe, but trends are less certain in Continental Europe. Projections for different definitions of drought by regional and global climate simulations show, with medium confidence, an increase in duration and intensity of droughts in Central Europe even in regions where summer precipitation is expected to increase as increased temperatures will impact evapotranspiration (Dezsi et al., 2018; IPCC, 2014; Stagge et al., 2017).

The aim of this study is to examine the effect of future climate change on the airborne birch pollen load in Central Europe. This has been achieved by modelling the impact of different climate change scenarios on the distribution and abundance of birch trees and the influence of short-term birch pollen production using the region of Bavaria in Southern Germany as a case study.

2 | MATERIALS AND METHODS

2.1 | Theoretical procedure

The novel methodological procedure detailed in this work integrates models for: (1) long-term changes in the spatial distribution and abundance of pollen sources; and (2) interannual changes in pollen

production associated with short-term meteorological variations (Figure 1). These models can be used to calculate the magnitude of airborne birch pollen concentrations and subsequent pollen exposure in the past (used for validation), near future and over the long term.

2.2 | Case study of birch: Pollen and climate datasets

We used the region of Bavaria (Southern Germany) as a case of study. Pollen data from 28 pollen stations were used in this study, with a maximum continuous time series of 30 years (i.e. in the city of Munich since 1989). Information about the aerobiological data used in this work is detailed in Figure S1. Pollen data were recorded using volumetric pollen traps of the Hirst (1952) design and following the minimum requirements described by the European Aerobiology Society (Galán et al., 2014). The pollen databases were managed using the 'AeRobiology' R package (Rojo et al., 2019) implemented in R Software (R Core Team, 2020). Pollen data were reported as daily average pollen concentrations (24 h period) and expressed as pollen grains/m³ of air. The yearly pollen amount was characterized using the API_n as the sum of the daily pollen concentrations ([pollen/m³]*day) during the year (Galán et al., 2017).

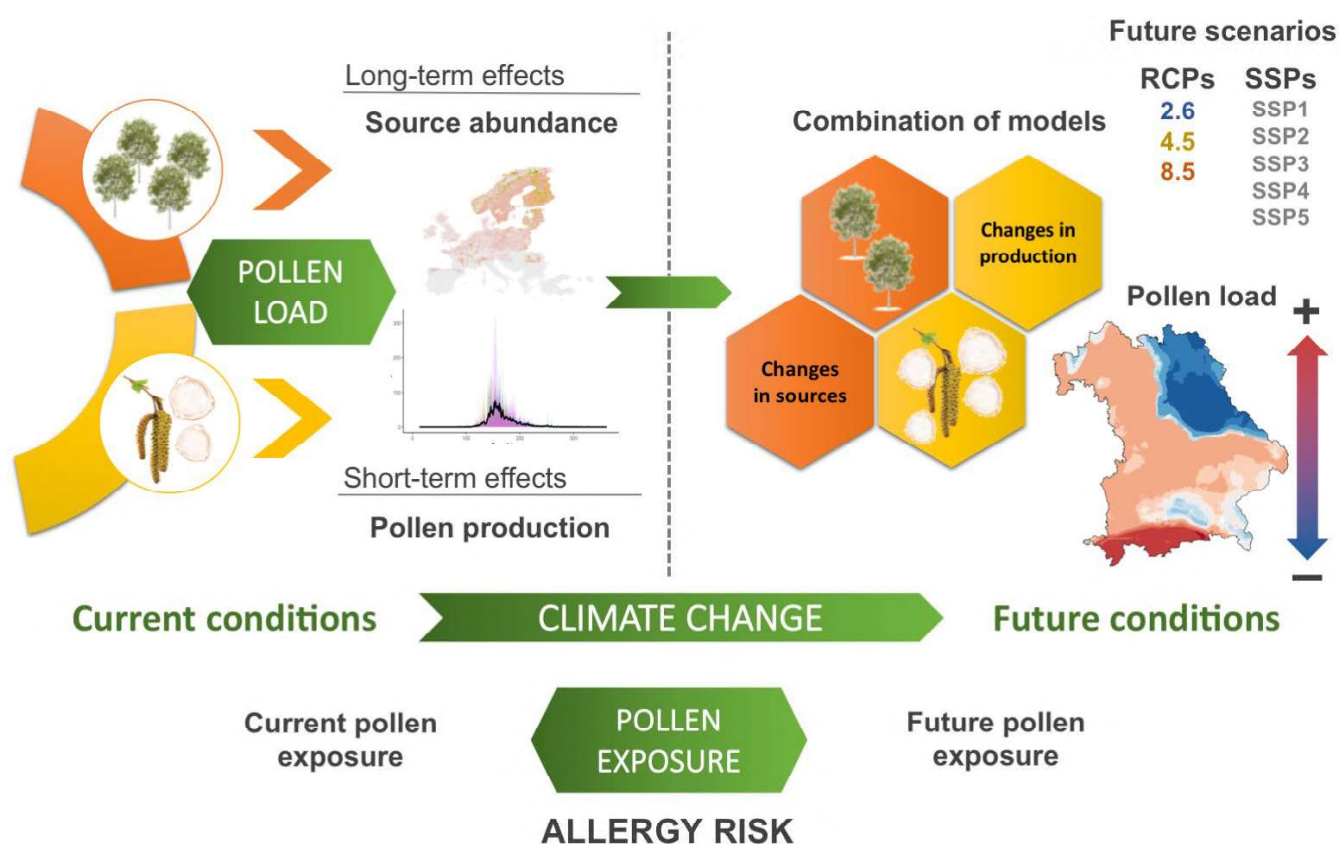


FIGURE 1 Theoretical procedure followed in the study for modelling the airborne birch pollen load and subsequent pollen exposure. RCPs, representative concentration pathways; SSPs, shared socioeconomic pathways [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Current climatic conditions (period 1989–2018) were provided by the daily gridded meteorological observations obtained from the E-OBS dataset from the EU-FP6 project UERRA (<http://www.uerra.eu>), the Copernicus Climate Change Service and the data providers of the ECA&D project (<https://www.ecad.eu>; Cornes et al., 2018).

For the future climatic conditions two main datasets were used:

1. Long-term patterns were analysed for the time periods 2050 (average for 2041–2060) and 2070 (average for 2061–2080) using future data provided by the World Climate Research Programme (WCRP) Phase 5 (CIMP5) (Working Group on Coupled Modelling, 2011) and processed by the Worldclim project (Fick & Hijmans, 2017) for the main general circulation models (GCMs) used in the IPCC Fifth Assessment Report (IPCC, 2014);
2. Short-term meteorological changes (annually for the period 2020–2100) were analysed using the daily regionalized data from the regional circulation models (RCMs) implemented by the Bavarian Environment Agency (Landesamt für Umwelt, LfU) in Southern Germany (Bayerisches Landesamt für Umwelt, 2020).

Detailed information about the GCMs and RCMs included in the models is included in Supporting information (Table S1). Three climate change scenarios (Representative Concentration Pathways—RCPs; van Vuuren et al., 2011) were used with potential radiative forcing of 2.6, 4.5 and 8.5 W/m².

2.3 | Modelling of pollen sources

A European map of birch tree abundance (percentage) was used to describe birch pollen sources. This map was provided as a relative probability of presence for the whole genus *Betula* in Europe by the European Atlas of Forest Tree Species. This resource is based on a European 1-km gridded dataset of birch tree abundance (percentage) derived from the national forest inventories of the European countries (De Rigo et al., 2016). The gridded datasets have been aggregated to the lower spatial resolution provided by the predictive variables (0.05° × 0.05°). Birch tree abundance at the European level was then also modelled based on predictors related to environmental and human factors; namely bioclimatic data, soil data, human pressure indicators and land use categories (see Figure S2). The model of the birch tree abundance allows birch abundance to be predicted in the future. Comparing current actual with current modelled birch tree distribution validated the model, which was then used to model birch tree abundance in the future.

Bioclimatic data to model the pollen sources were generated by monthly temperature and rainfall data and represent annual trends, seasonality and limiting environmental thresholds for plants (Busby, 1991). Specifically, 19 bioclimatic variables were employed as biologically meaningful variables (see Figure S2). The 'dismo' R package was used for their calculation (Hijmans et al., 2017). From an environmental point of view, soil taxonomy was also included as a

categorical predictor using the World Reference Base (Ribeiro et al., 2018).

The current anthropogenic effect on the birch abundance was modelled using both the Human Influence Index (HII) and a global land use dataset (Chen et al., 2020). The HII is an index of the global human footprint based on indicators of human pressure such as population density, the presence of communication infrastructures, land transformation and urban pressure in general (Sanderson et al., 2002). The map of anthropogenic impacts was provided in a 1-km gridded dataset (Wildlife Conservation Society-WCS & Center For International Earth Science Information Network-CIESIN-Columbia University, 2005). On the other hand, main land use classes were applied as predictors since vegetation types and land use classes work as good indicators of the presence of birch trees (Pauling et al., 2012). The main land use classes (forests, grasslands, crops, water, barren and urban) were obtained by reclassifying the 32 land types based on specific plant functional types (Chen et al., 2020), hence, the proportion by cell of each main land use was included as a predictor. Future changes in land uses were considered under diverse socioeconomic and climate scenarios. For this purpose, we used the global gridded land use dataset (0.05° × 0.05°) provided by Chen et al., (2020) generated using the Global Change Analysis Model under the three RCPs considered (2.6, 4.5 and 8.5 W/m²), and five shared socioeconomic pathways (SSPs) based on different alternative socioeconomic developments: sustainable development (SSP1), middle-of-the-road development (SSP2), regional rivalry (SSP3), inequality (SSP4) and fossil-fuelled development (SSP5; Riahi et al., 2017).

Several statistical methods were applied for modelling birch tree abundance, namely generalized linear model, partial least square regression (PLS), support vector machine (SVM) and random forest (RF). Most of these methods are commonly used ecological modelling techniques, although in this case a continuous variable (percentage) was modelled instead of a discrete variable (presence/absence) typical for species distribution models (Gobein et al., 2019; Scherrer et al., 2018). The statistical methods were evaluated in terms of greater accuracy of each model (the most accurate model was used in the following steps of the pollen load modelling).

Birch tree abundance was modelled for the whole of Europe (except Russia, Belarus and Ukraine) into which we embedded the other models specific for Bavaria. The model was trained for a random dataset composed of approximately 40% of the pixels (100,000 points). Our approach is based on a model of habitat suitability for birch abundance, which cannot be adjusted exactly with actual tree distributions for future projections due to limitations of migration rates (Prasad et al., 2020). We also compared our projection of pollen sources with the likelihood of colonization based on migration rates and habitat quality (See details of the methodological procedure in Figure S3 of Supporting information). The likelihood of colonization of birch in the region of Bavaria was calculated following the optimization and parametrization carried out by Prasad et al., (2013).

2.4 | Validation of the model of pollen sources

The most accurate modelling approach was RF, and different steps of validation of machine learning models were followed as shown in the Supporting information (Figure S4). The model of pollen sources was evaluated using both external validation and block validation. External validation is based on the evaluation of predictive capabilities of the model using the samples called 'out-of-bag' in RF technique. These samples are randomly selected and left out in each iterative training process (equivalent to cross-validation). One more restrictive step to ensure spatial independence of the predictions is block validation. In this case, each iteration is evaluated in a completely independent latitudinal area left out of the training process, and predictions are evaluated out of the spatial gradient used in model calibration. Specifically, 12 iterations were generated using 3-degree wide latitudinal bands at each iteration. This is particularly useful for future projections as the environmental gradient may be outside current conditions.

The variable importance of the model of pollen sources was evaluated using both the increase node purity (IncNodePurity) and the percentage increase in MSE (%IncMSE), provided by the 'randomForest' R package (Liaw & Wiener, 2002). The measurement of IncNodePurity for evaluating variable importance represents the number of times that one variable is used for the model for explaining the objective variable, while the %IncMSE is a measurement of exclusiveness of information that any other predictor could provide (Figure S4). Also, the individual effects of the most important variables were analysed using partial dependent plots provided by the 'pdp' R package (Brandon, 2017). These post hoc analyses allow the effect of the predictors to be analysed in machine learning techniques.

2.5 | Relationship between pollen sources and pollen load

The spatial birch tree abundance was related to the birch APIn using the concentric ring method developed by Oteros et al., (2015). The APIn for the Bavarian pollen stations with data from 2015 was correlated with the sum of birch tree abundance for every pixel within the concentric rings with a 5-km radius from the location of the stations until a maximum distance of 80 km. The relationships for every ring was used to generate a polynomial curve between the ring distance and the correlation coefficient with pollen amounts. The surface under the curve represents the theoretical influence of pollen emission from birch sources (i.e. birch trees) as a function of the abundance and distance of the sources. The equation of the curve was employed to calculate the specific influence index (SII) meaning the influence of the distribution of pollen sources around the stations. For more details of the procedure see Figure S5 in the Supporting information. Finally, a continuous layer with the SII was performed for every pixel for the entire area of the region of Bavaria, in this case applying a simplified concentric ring method with concentric rings of

10-km distance from one ring to another and with a maximum distance of 60-km radius to improve the computational speed of the SII calculation. SII was then used in the following steps of the modelling to predict the APIn.

Birch tree abundance was predicted for the future using the Worldclim bioclimatic datasets (Fick & Hijmans, 2017) from the CIMP5 (Working Group on Coupled Modelling, 2011) for the time periods 2050 and 2070. An ensemble using the median of the outputs for each of the GCMs proposed by the IPCC (2014) was generated for each RCPs considered (2.6, 4.5 and 8.5 W/m²) and for each shared socioeconomic pathways (SSP1, SSP2, SSP3, SSP4 and SSP5). Also, the standard deviation of the models may be consulted in the Supporting information (Figure S6) as a measure of the uncertainties of the climate models. The predicted birch tree abundance was used to estimate the future SII using the curve of the theoretical influence calculated by the concentric ring method. Although only SII values were calculated for current conditions and for two future periods, a smoothing spline interpolation was applied to obtain annual values as plant distribution changes represent a long-term process (Garcia et al., 2014).

2.6 | Modelling of pollen load

The APIn was modelled using different statistical approaches, namely PLS, SVM, Bayesian regularized neural network and RF. For each statistical method an algorithm was followed for selecting the most accurate model. This process is schematized in Figure S7 (Supporting information). The dataset used was the full pool of stations and years available for this study. The APIn for each case (stations × years) was the response variable, and monthly and seasonal meteorological data for current and previous year were included as predictors. Also, the SII index described above was included as a predictor, characterizing the influence of the birch pollen sources for each pollen station. The statistical algorithm corresponds to an iterative process that was repeated five times where a training (75% of cases) and testing set (25% of cases) were randomly selected. In each iteration, a backward selection process of variables was applied and the predictor with the lowest value of variable importance was removed. The best model was selected based on three validation processes, namely internal validation, threefold cross-validation and external validation of 25% of independent cases (the most accurate model was shown). Models were quantified using three indexes (coefficient of determination R^2 between estimated and observed values, root mean square error—RMSE and mean absolute error—MAE).

2.7 | Past reconstruction and future projections

The best model, in terms of accuracy obtained by the integrative approach for both long-term changes in pollen sources and short-term changes in pollen production, was validated using past data and used to make projections for the future. The reconstruction of

past birch APIn for the Bavaria region was calculated annually for a 30-year period (1989–2018) following a spatio-temporal prediction using the observed climate datasets (E-OBS datasets; see Figure S8 in Supporting information). The model was then applied to the period 1975–2100 using the future climate dataset from the different RCMs provided by the Bavarian Environment Agency described previously. After applying the model of pollen load, a 30-year moving average of calculated APIn was used to obtain long-term projections. An ensemble model was calculated by the median value of the outputs for each of the RCMs, and only one model was retrieved from all RCMs. Values of standard deviation of the model are shown in the Supporting information (Figure S6).

3 | RESULTS

3.1 | Modelling of pollen sources

The birch tree abundance data provided by the European Atlas of Forest Tree Species were modelled by a RF technique, as this turned out to be the most accurate model. This model was trained in 100,000 points throughout Europe retrieving a coefficient of determination $R^2 = 0.84$ for external validation (~cross-validation; Figure S4). Figure 2a shows the results of the model in Europe and the region of Bavaria in Germany respectively. Future projections for birch abundance in Europe showed a decrease in birch abundance at lower altitudes of Central Europe while an increase was projected in the Alps. Also, an increase in birch abundance was projected in the Northern limits of the European birch distribution (Figure 2). In Bavaria all scenarios, to a greater or lesser extent, showed an increase in birch abundance towards the South, and a decrease in the Northeast of Bavaria, where the species is now abundant.

The variables with a positive influence on the abundance of birch were percentage of forest cover, which was the most important variable based on land use, and precipitation during the warmest period. On the other hand, variables with a negative influence on birch abundance were the HII, based on indicators of human pressure, and the bioclimatic indices annual mean temperature and isothermality that highlighted the negative influence of temperature and seasonality on birches in the model (detailed information about validation and variable importance may be consulted in the Supporting information, Figure S4).

The relationships between the distribution and abundance of birch trees and airborne pollen load were studied using the concentric ring method (Figure S5). The most important factor, the SII, was based on the polynomial curve that represents the correlations between the birch tree abundance and pollen amounts in concentric rings (Figure 3). In this study, the fitted statistical curve had $R^2 = 0.87$ ($p < 0.001$). When the SII was calculated and compared with the APIn for the year 2015 (when the most stations were operated), the relationship between SII and APIn resulted in a coefficient of determination of $R^2 = 0.66$ ($p < 0.001$; Figure 3).

3.2 | Modelling of pollen load

The best statistical method for predicting birch APIn in the Bavaria region was also RF with the most important predictive variable being SII based on the variable importance index (Figure S7). Other predictors for APIn accounting for a lower variable importance were climatic variables, the most important of which being precipitation in the previous spring and minimum temperature in the previous summer and autumn. Meteorological conditions of the previous autumn and during the pollen season (month of April) had some relevance. However, winter seemed to be the least relevant period for birch APIn. The statistical model generated had $R^2 = 0.94$ ($\text{MAE} = 892 \text{ pollen/day} \cdot \text{m}^3$), and the external validation over the random 25% of the independent cases retrieved a coefficient of determination of $R^2 = 0.76$ ($\text{MAE} = 1678 \text{ pollen/day} \cdot \text{m}^3$). Figure 4 shows the fitting of the model for the entire dataset (stations \times years) indicating whether the value was included in the training set or used for externally testing of the model.

3.3 | Validation

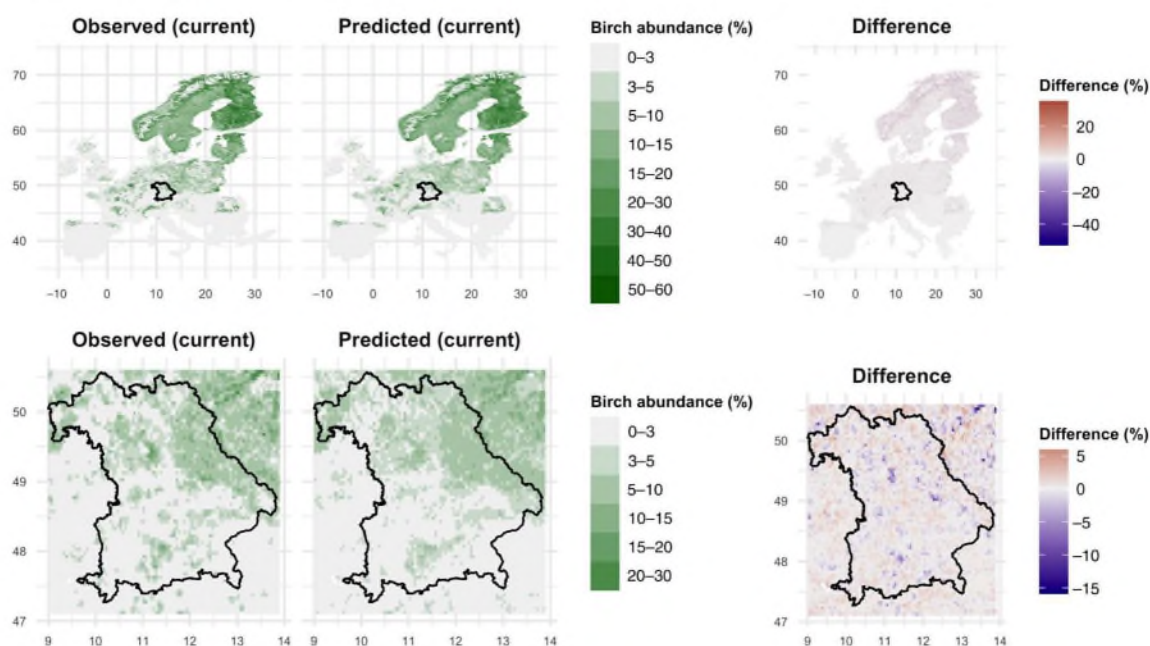
The selected statistical model was applied to past data for validation and was used to make projections for the future. The APIn for every year was reconstructed for the entire Bavaria region for the period 1989–2018 (the results of the validation in the past may be consulted in Supporting information, Figure S8). For this 30-year period, trend analysis shows an increase in pollen amounts over the entire territory and only slight decreases were obtained in limited areas in the North. However, the significant slopes were mainly distributed in the Southwest of Bavaria in the vicinity of the Alps (Figure S8).

3.4 | Future projections

The strongest influence on pollen load in the region of Bavaria is provided by birch abundance (presence of pollen sources) and, to a lesser extent, the effect of climate (Figure 5). The North-eastern part of Bavaria is projected to experience the sharpest decrease in birch APIn. Airborne birch pollen concentration in the mid-South of Bavaria may increase slightly under all RCPs, as a consequence of the increase in the habitat suitability for birch, especially in the central part of this area. Taking into account limitations in migration rates, the most dramatic increases in birch APIn are likely to be restricted to the Southern fringes of Bavaria (Figure S9).

Future changes in birch APIn for three RCPs (ensemble projections for the five SSPs) are shown for the whole of Bavaria (Figure 6) and in more detail for individual stations (Figure 7). The results show a clear decrease in birch APIn in Northern parts of Bavaria. This decline is most prominent in the Northeast and especially for RCP 8.5. As can be seen for DEBAYR (Bayreuth), in the Northeast of Bavaria, these decreases are projected to stabilize towards the end of the century for RCPs 2.6 and RCPs 4.5 ($\sim 5000 \text{ pollen/day} \cdot \text{m}^3$), but not

(a) Modelling in current conditions



(b) Projected in future conditions

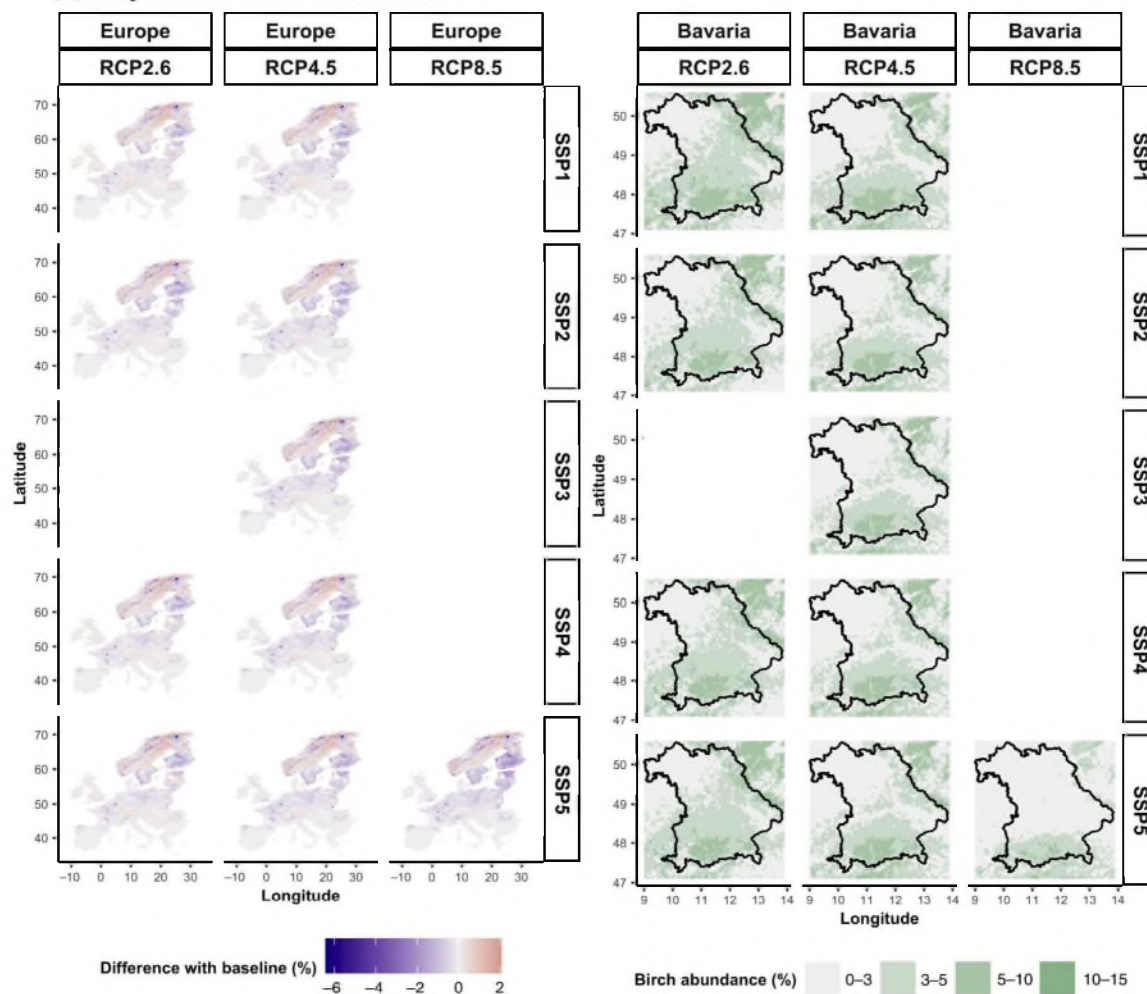


FIGURE 2 (a) Observed versus modelled current birch tree abundance of Europe (top) and in the region of Bavaria in Southern Germany (bottom); (b) Projected birch abundance, difference from the baseline in Europe (left) and projected birch abundance in the region of Bavaria (right) under different representative concentration pathways (RCPs) and shared socioeconomic pathways (SSPs) [Colour figure can be viewed at wileyonlinelibrary.com]

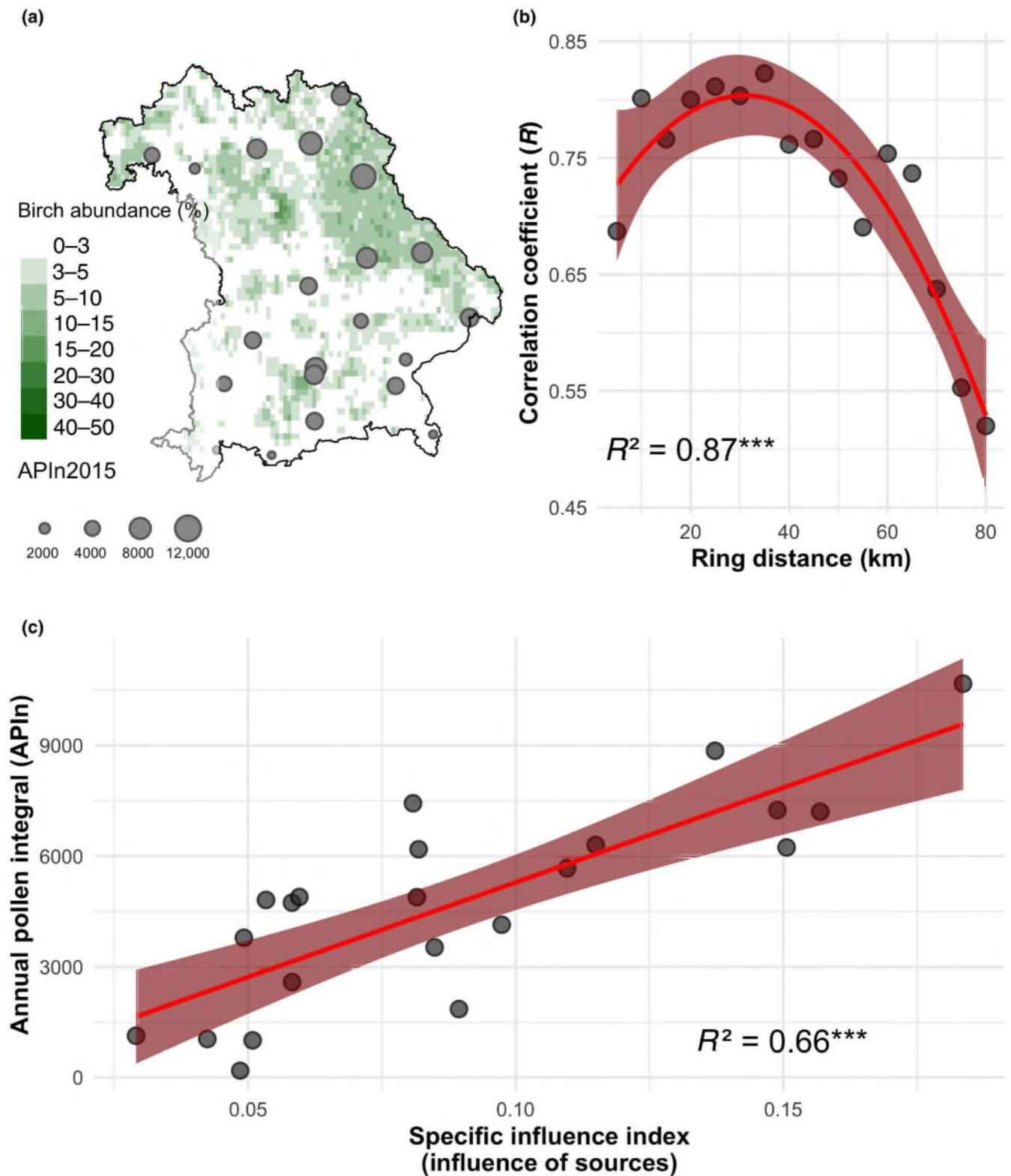


FIGURE 3 Results of the concentric ring method for current conditions. (a) Available pollen stations with complete databases during 2015; (b) Polynomial curve of the theoretical influence of the pollen emission as a function of the abundance and the distance of the sources; (c) Relationship between specific influence index and annual pollen integral. Significance levels: $***p < 0.001$ [Colour figure can be viewed at wileyonlinelibrary.com]

for RCP 8.5. For RCP 4.5 in DEMUNC (Munich) an initial increase in birch APIn is projected to be followed by a decrease towards the

end of the century. In areas of higher elevation around the Alps, an increase in birch APIn is generally expected for all climate change

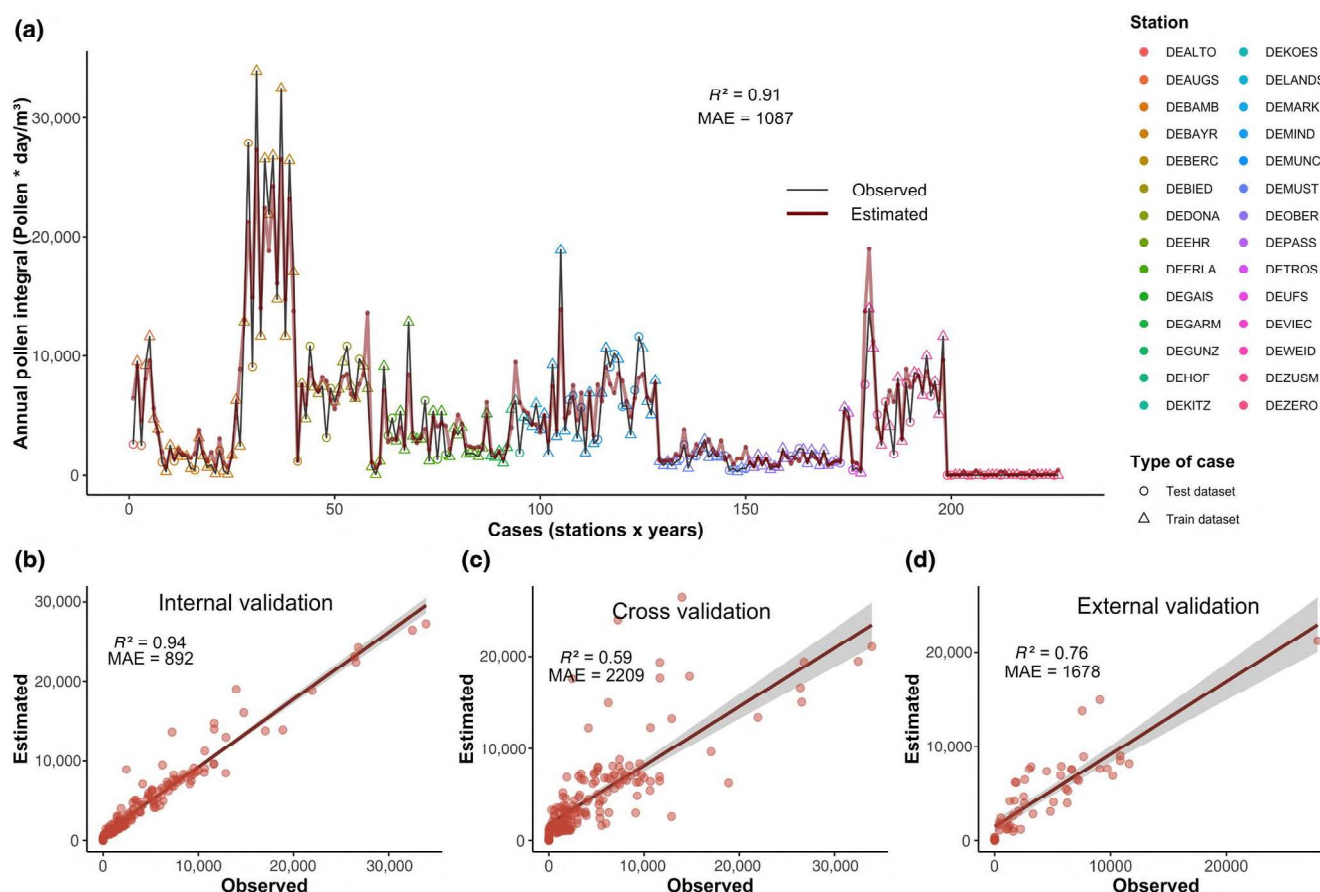


FIGURE 4 Validation of the statistical model for predicting the intensity of birch annual pollen integral: (a) All cases are shown for all stations and all years; (b) internal validation; (c) cross-validation; (d) external validation with independent cases (subset of 25% of the total cases) [Colour figure can be viewed at wileyonlinelibrary.com]

scenarios, as exemplified by DEOBER (Oberjoch). This pattern is already evident in the Southwest of the territory as shown by trends observed during the last three decades (Figure S8), and this trend is expected to continue towards the end of the century due to increased likelihood of colonization (Figure S9). Partial results of this work are shown in www.klimapollen.de.

4 | DISCUSSION

Birch is a dominant tree species in Northern Europe. In Central Europe, for example, the region of Bavaria, birch is less dominant and occurs as part of the mixed forests with coniferous species such as Norway spruce (*Picea abies*) and pine (*Pinus* spp.) and broadleaved species like beech (*Fagus sylvatica*) and oak (*Quercus* spp.; Hynynen et al., 2010) as well as sporadically in the open landscape. In this study, both *B. pendula* and *B. pubescens* were spatially modelled together, as the pollen grains of the two species are microscopically indistinguishable from one another. Both birch species present differences in ecological requirements since *B. pendula* requires drier and more fertile soils than *B. pubescens* and, from a climatic point of view, *B. pubescens* is more tolerant of colder northern conditions

whereas *B. pendula* withstands relatively warmer conditions in the South (Atkinson, 1992; Beck et al., 2016). However, they are similarly limited by high temperatures and low water availability during the warmest period of the year (Myking & Heide, 1995; Noce et al., 2017; Rubio-Cuadrado et al., 2018).

We combined two models; one for birch pollen sources (birch trees) and the other for birch pollen load (APIn). The predictors explaining the greatest variance in the spatial modelling of birch abundance were the cover of forests and indicators of human pressure, and the bioclimatic variables annual mean temperature, seasonality and precipitation during the warmest months (Figure S10 shows predicted climate changes in the whole of Europe). Human activity has profoundly perturbed the landscape since ancient times (Leuschner & Ellenberg, 2017) and in Central Europe the surfaces dedicated to agricultural fields, pastures for cattle and urban infrastructure have changed the configuration of the forests in the territory (Wade et al., 2003; Wan et al., 2018). In the model for APIn, the most important factor determining airborne birch pollen was the SII, that is, the number and distance of surrounding birch trees.

Birch populations in Mediterranean areas are at the edge of the respective distributions, and so are the most vulnerable to changes in climate conditions (Noce et al., 2017). Bavaria, in Southern Germany,

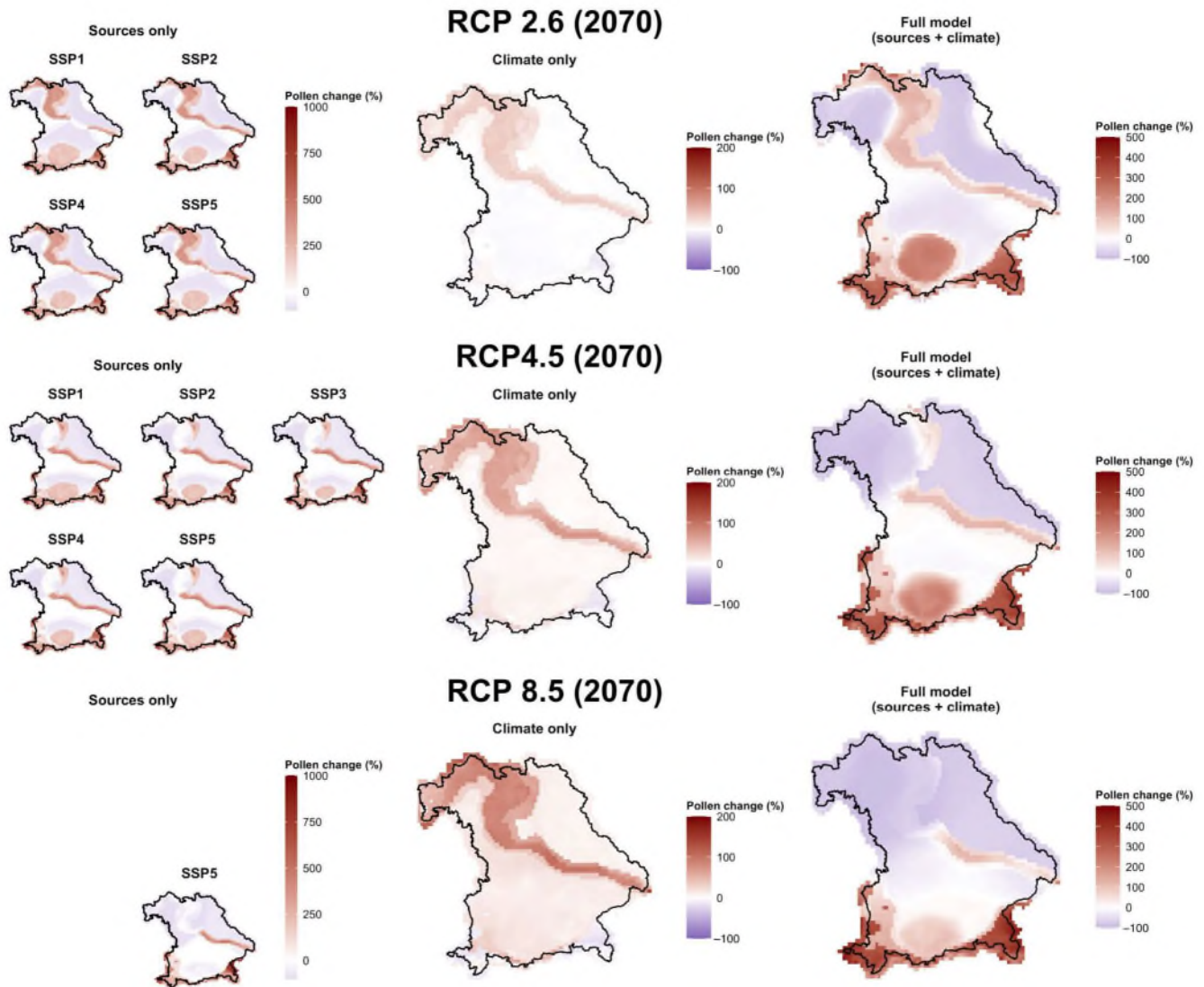


FIGURE 5 Differences between birch annual pollen integral projected in the future (2070) and the baseline (1989–2018), taking into account independent effects of the change in pollen sources (long-term effect), the change in climate conditions (short-term effect) and full effect (integrative model). Note that the scale of the legend differs for the effects because the magnitude of change is very different [Colour figure can be viewed at wileyonlinelibrary.com]

can be considered as being in an intermediate position as its birch occurrences are in areas with the least habitat suitability for birch trees in the entire German territory (Beck et al., 2016). The distribution of birch species in southern and mid-latitudes of Europe will suffer displacements towards more northern and higher elevated areas by the end of the 21st century (Dyderski et al., 2018). In this study, all scenarios for future climate change in Bavaria project the same direction of change, with birches suffering notable declines in the lowlands of the Northwest of the region and the Danube valley. The most pessimistic scenarios project a drastic decline in the Northeast, where birch trees have a higher relative share of the forest cover, and a displacement towards areas of higher elevation like the slopes of Alps in the South. However, a more specific approach based on migration rate reveals a slower displacement of birch trees to the South resulting in only gradual increases in pollen load

towards the highlands of the Alps (Prasad et al., 2020). Moreover, birch trees could persist in areas not particularly suited for reproduction due to plasticity and local adaptability as well as due to more disturbance events (Fréjaville et al., 2020). Although climate change could also provoke a decrease in pollen production in these areas. Southwestern areas of Bavaria are projected to exhibit the greatest increases in pollen load, and a significant positive trend in APIn has already been observed in this area over the last three decades based on our results as well as other European areas (Ziello et al., 2012).

The impacts of projected climate changes on future birch tree distribution are significant. First, there are obvious ecological consequences associated with the changes in forest ecosystems (Morin et al., 2018; Thom et al., 2017). For instance, birch species play a key role in ecosystems as pioneers during early stages of forest establishment and therefore the decline of birches reduces the resilience

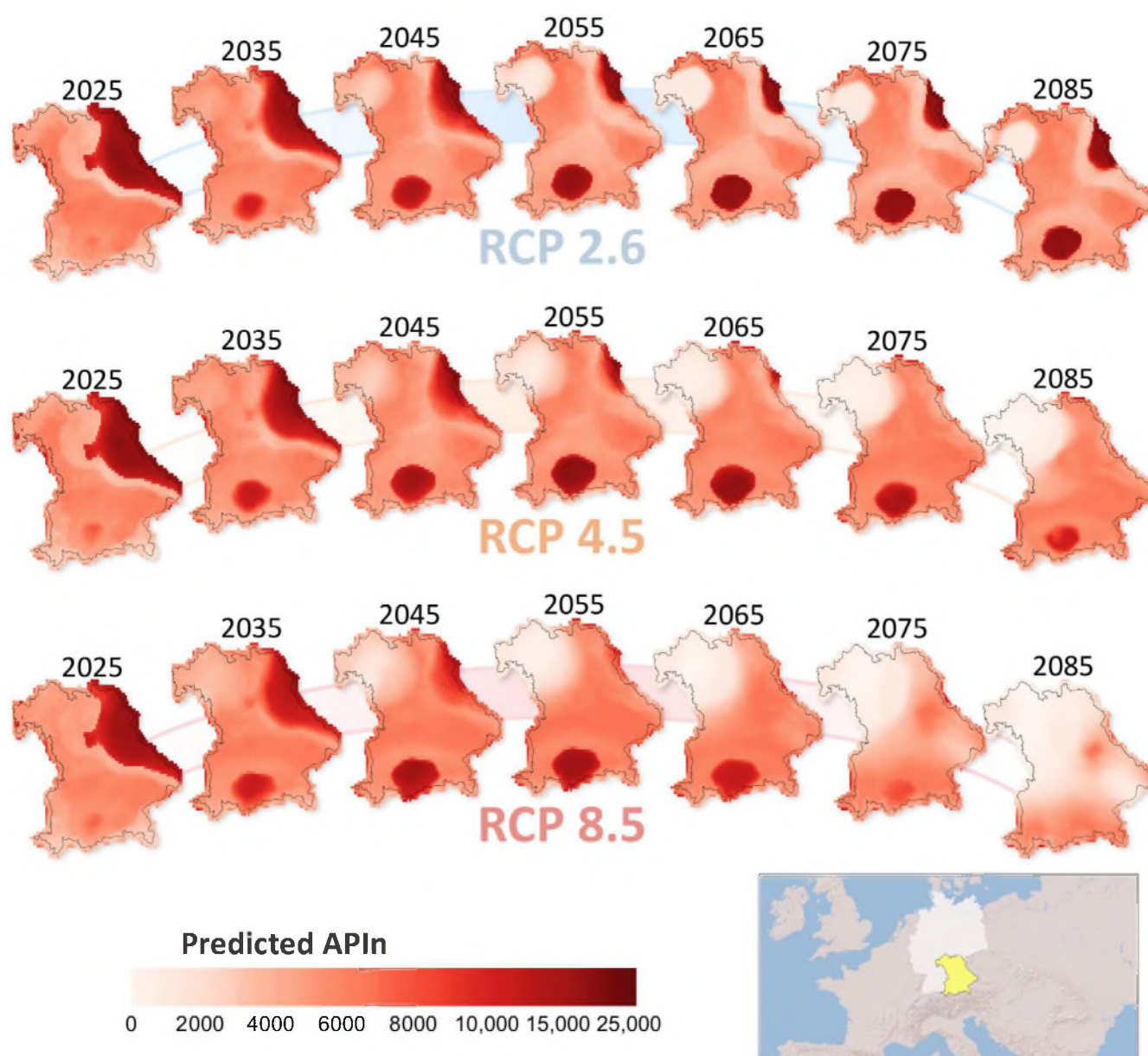


FIGURE 6 Future projections of birch annual pollen integral (APIn) in Bavaria (Germany) according to the climate change scenarios considered (representative concentrations pathways—RCPs). Potential radiative forcing of 2.6, 4.5 and 8.5 W/m² [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

of forests under natural or anthropogenic disturbances (Leuschner & Ellenberg, 2017). Beyond the impacts on ecological systems, birch displacements have important repercussions for public health, with increases or decreases in pollen exposure depending on the geographical area. For most of Bavaria, the number of birch trees and the amount of airborne birch pollen will decline at the end of the century, but firstly increasing, which agrees with the reported by previous results (Rojo et al., 2021).

Birch pollen is the dominant allergenic pollen type in Central and Northern European areas (Burbach et al., 2009; Smith et al., 2014). Birch pollen can travel very long distances in the atmosphere (Bogawski et al., 2019; Menzel et al., 2021), but most pollen is dispersed at local and regional spatial scales (Sofiev, 2017). The

results of this study also show that birch trees distributed within the first 30 km surrounding the samplers exerted the greatest influence on the amounts of airborne birch pollen collected. Therefore, the distance from the pollen sources (i.e. birch trees) determines the potential exposure to pollen and the potential allergic risk for the sensitized population. This aspect is even more relevant in birches, as this tree species is frequently cultivated as an ornamental in temperate cities. While specific studies showed the influence of ornamental birch trees in urban areas as relevant sources of pollen (Skjøth et al., 2008), the regional spatial scale of our model for birch pollen abundance seems to be independent to this very local effect. Pollen dispersal of urban trees would have a great effect in areas very close to trees (Adams-Groom et al., 2017), but the main

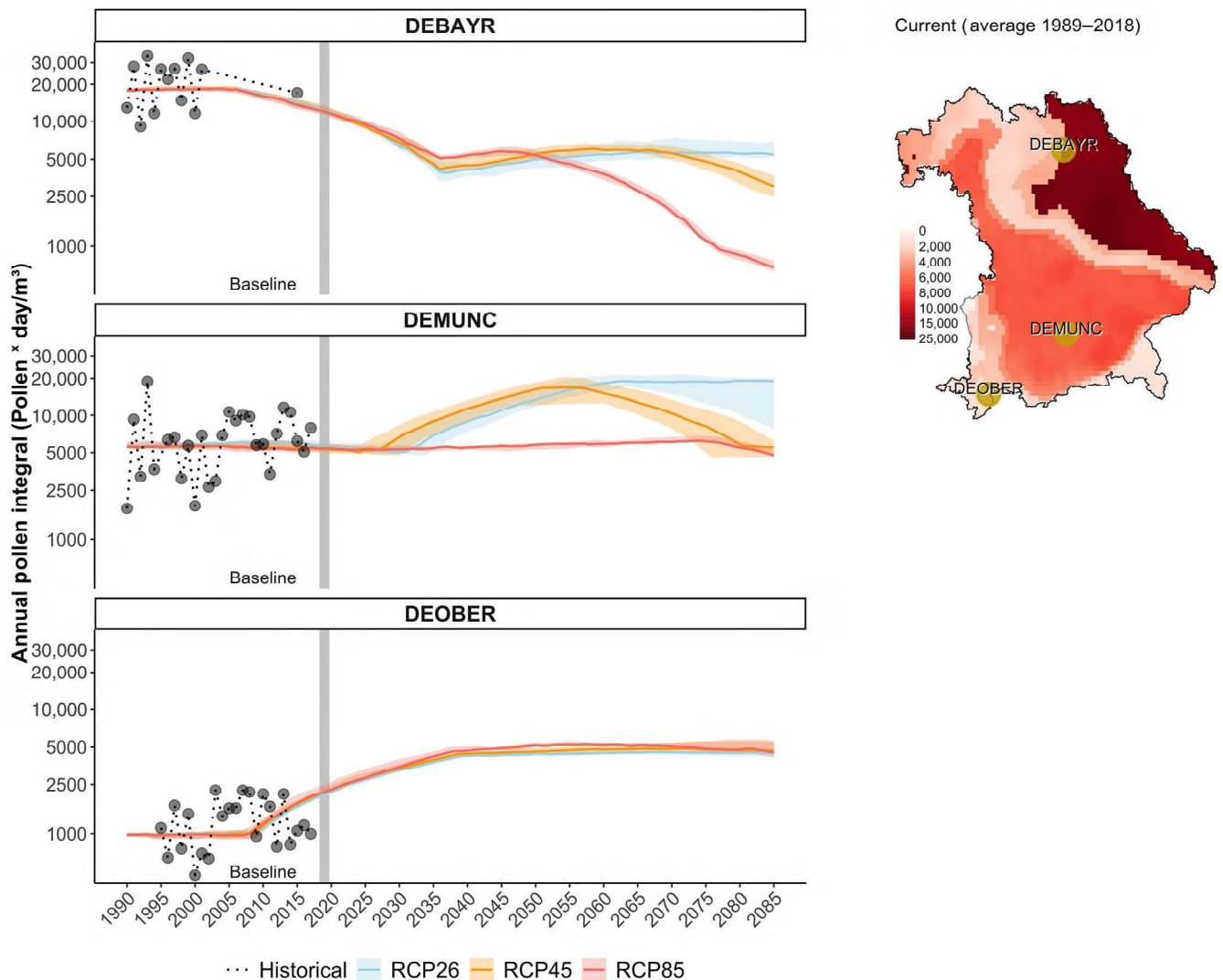


FIGURE 7 Future projections of birch annual pollen integral (APIn) for three specific sites in Bavaria (DEBAYR, Bayreuth; DEMUNC, Munich; and DEOBER, Oberjoch) according to the representative concentrations pathways (RCPs) considered (2.6, 4.5 and 8.5 W/m²; left), and percentage of change of the birch pollen for two RCPs (2.6 and 8.5; right). The confidence intervals (on the left) represent the maximum and minimum predicted value of APIn for the different regional circulation models. The thick line represents the median value of all these predictions [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

background amounts of birch pollen could come from more distant areas (explaining the relevance of the forests areas to model pollen load), and would explain why airborne birch pollen concentrations are not dependent on the location of the pollen traps within cities (Bastl et al., 2019; Rojo et al., 2020).

The relationship between the abundance of birch trees, estimated as the SII in this work (see methodological procedure of the Concentric Ring Method (Oteros et al., 2015)), and airborne birch pollen loads is clear and linear. On the other hand, pollen production in arboreal species is positively influenced by temperature (temperature of the previous summer and autumn as obtained in the results) and increases in atmospheric CO₂ (Darbah et al., 2008; Ziska et al., 2019). Indeed, previous studies showed positive significant trends in birch pollen production in Central and Northern Europe as a response to higher temperatures during the favourable growing

seasons (Frei & Gassner, 2008; Lind et al., 2016). According to our results, trends towards higher birch APIn over the last 30 years were shown in Bavaria, but trends are only significant in the Southwest of the region, where an increase in pollen load was projected for the future. However, this behaviour is not generalized, and trends in birch APIn are site dependent (Marchand et al., 2020; Ziello et al., 2012).

Statistical methods assuming non-linear effects of the predictors, such as the influence of meteorology (Zhang et al., 2015), are crucial for modelling birch APIn. The machine learning method of regression such as RF was successful in this work, and obtained the most accurate results. RF techniques have increased their popularity for modelling spatiotemporal environmental variables in recent years due to their accuracy (Bogawski et al., 2019; Mendoza & Araújo, 2019; Zhang et al., 2020). Furthermore, the integrative approach proposed in this work for modelling airborne birch pollen

load incorporates both future long-term changes in the distribution of birch trees and changes in the production of birch pollen caused by short-term meteorological changes (which will also change in the long term). Our procedure allows for projections to be made about pollen exposure by taking into account the effects of climate change at the population level (pollen sources) and relates to the ecophysiological level of the plant (pollen production) (Garcia et al., 2014).

5 | CONCLUSIONS

This study shows that anthropogenic induced climate change will have a marked impact on the exposure of the allergic population to airborne birch pollen in Central Europe. Using Bavaria in Southern Germany as a case study, we used a novel methodological procedure to model the birch APIn that employs both long-term changes in the spatial distribution and abundance of birch trees and interannual changes in the production of birch pollen associated with short-term meteorological variations. The integrated model shows that climate change will result in a decrease in airborne birch pollen in the North of Bavaria, particularly in the Northeast where most birch trees are currently distributed. Elsewhere in Bavaria, warmer summer temperatures will initially favour birch pollen production and result in more severe birch pollen seasons. However, this early increase in airborne birch pollen is projected to be followed by a decline in exposure towards the end of the 21st century as climate change impacts birch tree distribution. Conversely, the burden of birch pollen allergy may shift to areas of higher elevation as birches become more abundant in these areas. The integrative modelling approach used in this study may be extended to other areas and other plant species. The ecological drivers of plant distribution and pollen production differ between plant species, and knowledge about these processes is important for understanding the impacts of climate change on the health of the population. For birch we could show that climate change will initially increase airborne birch pollen load, but then later in the century reduce the number of birch trees (sources of pollen) resulting in a decrease in birch pollen exposure in most areas of the region of Bavaria.

ACKNOWLEDGEMENTS

We thank the ZAUM team who managed the manual work for Biederstein 2003–2018 and the ePIN network all over Bavaria in 2015: Christine Weil, Elke Bartusel, Cordula Ebner von Eschenbach, Gudrun Pusch, Robert Gebauer and Norbert Ertl. We thank the team of the German Pollen Information Service Foundation for the long time series of pollen data, and the Alpenklinik Santa Maria for pollen data from Oberjoch. We also thank the team of the Prof. Sabine Timpf for the visualization of the results in the project. We are grateful to Dr. Manuel Mendoza for the support with the machine learning procedures, and Dr. Min Chen for providing the global land use datasets. Dr. A. Picornell was supported by a predoctoral grant financed by the Ministry of Education, Culture and Sport of Spain, in the Program for the Promotion of Talent and its Employability

(FPU15/01668). We thank the Bavarian Health and Food Safety Authority (LGL), Munich, Germany for coordinating ePIN and coordinating the availability of the pollen data. Also, we thank the Bavarian Environment Agency (Landesamt für Umwelt, LfU) for providing the regional climate projections.

CONFLICT OF INTEREST

The authors declare they have no actual or potential competing financial interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the authors upon reasonable request. The data are not publicly available due to privacy or ethical restrictions.

ORCID

Jesús Rojo  <https://orcid.org/0000-0002-3627-130X>
 Jose Oteros  <https://orcid.org/0000-0002-9369-8633>
 Antonio Picornell  <https://orcid.org/0000-0002-3102-1344>
 José M. Maya-Manzano  <https://orcid.org/0000-0003-3595-0949>
 Athanasios Damialis  <https://orcid.org/0000-0003-2917-5667>
 Matthias Werchan  <https://orcid.org/0000-0002-9251-2016>
 Barbora Werchan  <https://orcid.org/0000-0002-6596-2011>
 Matt Smith  <https://orcid.org/0000-0002-4170-2960>
 Annette Menzel  <https://orcid.org/0000-0002-7175-2512>
 Sabine Timpf  <https://orcid.org/0000-0002-7964-4110>
 Claudia Traidl-Hoffmann  <https://orcid.org/0000-0001-5085-5179>
 Karl-Christian Bergmann  <https://orcid.org/0000-0002-0306-9922>
 Carsten B. Schmidt-Weber  <https://orcid.org/0000-0002-3203-8084>
 Jeroen Buters  <https://orcid.org/0000-0003-3581-5472>

REFERENCES

- Adams-Groom, B., Skjøth, C. A., Baker, M., & Welch, T. E. (2017). Modelled and observed surface soil pollen deposition distance curves for isolated trees of *Carpinus betulus*, *Cedrus atlantica*, *Juglans nigra* and *Platanus acerifolia*. *Aerobiologia*, 33(3), 407–416. <https://doi.org/10.1007/s10453-017-9479-1>
- Atkinson, M. D. (1992). *Betula pendula* Roth (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. *Journal of Ecology*, 80(4), 837–870. <https://doi.org/10.2307/2260870>
- Bastl, M., Bastl, K., Karatzas, K., Aleksic, M., Zetter, R., & Berger, U. (2019). The evaluation of pollen concentrations with statistical and computational methods on rooftop and on ground level in Vienna – How to include daily crowd-sourced symptom data. *World Allergy Organization Journal*, 12(5), 100036. <https://doi.org/10.1016/j.waojou.2019.100036>
- Bayerisches Landesamt für Umwelt. (2020). *Bayerische Klimadaten—Beobachtungsdaten, Klima-projektionsensemble und Klimakennwerte für Bayern*, Augsburg: 12 S.
- Beck, P., Caudullo, G., de Rigo, D., & Tinner, W. (2016). *Betula pendula*, *Betula pubescens* and other birches in Europe: Distribution, habitat, usage and threats. In J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant, & A. Mauri (Eds.), *European atlas of forest tree species* (pp. 70–73). Publication Office of the European Union.

- Biedermann, T., Winther, L., Till, S. J., Panzner, P., Knulst, A., & Valovirta, E. (2019). Birch pollen allergy in Europe. *Allergy*, 74(7), 1237–1248. <https://doi.org/10.1111/all.13758>
- Bogawski, P., Borycka, K., Grewling, Ł., & Kasprzyk, I. (2019). Detecting distant sources of airborne pollen for Poland: Integrating back-trajectory and dispersion modelling with a satellite-based phenology. *Science of the Total Environment*, 689, 109–125. <https://doi.org/10.1016/j.scitotenv.2019.06.348>
- Bogawski, P., Grewling, Ł., & Jackowiak, B. (2019). Predicting the onset of *Betula pendula* flowering in Poznań (Poland) using remote sensing thermal data. *Science of the Total Environment*, 658, 1485–1499. <https://doi.org/10.1016/j.scitotenv.2018.12.295>
- Brandon, M. (2017). pdp: An R package for constructing partial dependence plots. *The R Journal*, 9, 421. <https://doi.org/10.32614/RJ-2017-016>
- Burbach, G. J., Heinzerling, L. M., Edenharter, G., Bachert, C., Bindslev-Jensen, C., Bonini, S., Bousquet, J., Bousquet-Rouanet, L., Bousquet, P. J., Bresciani, M., Bruno, A., Canonica, G. W., Darsow, U., Demoly, P., Durham, S., Fokkens, W. J., Giavi, S., Gjomarkaj, M., Gramiccioni, C., ... Zuberbier, T. (2009). GA² LEN skin test study II: Clinical relevance of inhalant allergen sensitizations in Europe. *Allergy*, 64(10), 1507–1515. <https://doi.org/10.1111/j.1398-9995.2009.02089.x>
- Busby, J. (1991). BIOCLIM – A bioclimate analysis and prediction system. *Plant Protection Quarterly*, 61, 8–9.
- Buters, J. T. M., Thibaudon, M., Smith, M., Kennedy, R., Rantio-Lehtimäki, A., Albertini, R., Reese, G., Weber, B., Galán, C., Brandao, R., Antunes, C. M., Jäger, S., Berger, U., Celenk, S., Grewling, Ł., Jackowiak, B., Sauliene, I., Weichenmeier, I., Pusch, G., ... Cecchi, L. (2012). Release of Bet v 1 from birch pollen from 5 European countries. Results from the HIALINE study. *Atmospheric Environment*, 55, 496–505. <https://doi.org/10.1016/j.atmosenv.2012.01.054>
- Chen, M., Vernon, C. R., Graham, N. T., Hejazi, M., Huang, M., Cheng, Y., & Calvin, K. (2020). Global land use for 2015–2100 at 0.05° resolution under diverse socioeconomic and climate scenarios. *Scientific Data*, 7(1), 2015–2100. <https://doi.org/10.1038/s41597-020-00669-x>
- Cornes, R. C., van der Schrier, G., van den Besselaar, E. J. M., & Jones, P. D. (2018). An ensemble version of the E-OBS temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123(17), 9391–9409. <https://doi.org/10.1029/2017JD028200>
- Darbah, J. N. T., Kubiske, M. E., Nelson, N., Oksanen, E., Vapaavuori, E., & Karnosky, D. F. (2008). Effects of decadal exposure to interacting elevated CO₂ and/or O₃ on paper birch (*Betula papyrifera*) reproduction. *Environmental Pollution*, 155(3), 446–452. <https://doi.org/10.1016/j.envpol.2008.01.033>
- De Rigo, D., Caudullo, G., Houston Durrant, T., & San-Miguel-Ayán, J. (2016). *The European atlas of forest tree species: Modelling, data and information on forest tree species*. European Atlas of Forest Tree Species.
- Dezsi, Ş., Mîndrescu, M., Petrea, D., Rai, P. K., Hamann, A., & Nistor, M.-M. (2018). High-resolution projections of evapotranspiration and water availability for Europe under climate change. *International Journal of Climatology*, 38(10), 3832–3841. <https://doi.org/10.1002/joc.5537>
- Drobyshev, I., Guitard, M.-A., Asselin, H., Genries, A., & Bergeron, Y. (2014). Environmental controls of the northern distribution limit of yellow birch in eastern Canada. *Canadian Journal of Forest Research*, 44(7), 720–731. <https://doi.org/10.1139/cjfr-2013-0511>
- Dyderski, M. K., Paź, S., Frelich, L. E., & Jagodziński, A. M. (2018). How much does climate change threaten European forest tree species distributions? *Global Change Biology*, 24(3), 1150–1163. <https://doi.org/10.1111/gcb.13925>
- Fawcett, A. A., Iyer, G. C., Clarke, L. E., Edmonds, J. A., Hultman, N. E., McJeon, H. C., Rogelj, J., Schuler, R., Alsalam, J., Asrar, G. R., Creason, J., Jeong, M., McFarland, J., Mundra, A., & Shi, W. (2015). Can Paris pledges avert severe climate change? *Science*, 350(6265), 1168–1169. <https://doi.org/10.1126/science.aad5761>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Frei, T., & Gassner, E. (2008). Climate change and its impact on birch pollen quantities and the start of the pollen season an example from Switzerland for the period 1969–2006. *International Journal of Biometeorology*, 52(7), 667–674. <https://doi.org/10.1007/s00484-008-0159-2>
- Fréjaville, T., Vizcaíno-Palomar, N., Fady, B., Kremer, A., & Garzón, M. B. (2020). Range margin populations show high climate adaptation lags in European trees. *Global Change Biology*, 26(2), 484–495. <https://doi.org/10.1111/gcb.14881>
- Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J., Song, Y., Vitasse, Y., Zeng, Z., & Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, 526(7571), 104–107. <https://doi.org/10.1038/nature15402>
- Galán, C., Ariatti, A., Bonini, M., Clot, B., Crouzy, B., Dahl, A., Fernandez-González, D., Frenguelli, G., Gehrig, R., Isard, S., Levetin, E., Li, D. W., Mandrioli, P., Rogers, C. A., Thibaudon, M., Sauliene, I., Skjoth, C., Smith, M., & Sofiev, M. (2017). Recommended terminology for aerobiological studies. *Aerobiologia*, 33(3), 293–295. <https://doi.org/10.1007/s10453-017-9496-0>
- Galán, C., Smith, M., Thibaudon, M., Frenguelli, G., Oteros, J., Gehrig, R., Berger, U., Clot, B., Brandao, R., & EAS QC Working Group. (2014). Pollen monitoring: Minimum requirements and reproducibility of analysis. *Aerobiologia*, 30(4), 385–395. <https://doi.org/10.1007/s10453-014-9335-5>
- García, R. A., Cabeza, M., Rahbek, C., & Araujo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344(6183), 1247579. <https://doi.org/10.1126/science.1247579>
- Giesecke, T., Wolters, S., van Leeuwen, J. F. N., van der Knaap, P. W. O., Leydet, M., & Brewer, S. (2019). Postglacial change of the floristic diversity gradient in Europe. *Nature Communications*, 10(1), 5422. <https://doi.org/10.1038/s41467-019-13233-y>
- Gobeyn, S., Mouton, A. M., Cord, A. F., Kaim, A., Volk, M., & Goethals, P. L. M. (2019). Evolutionary algorithms for species distribution modelling: A review in the context of machine learning. *Ecological Modelling*, 392, 179–195. <https://doi.org/10.1016/j.ecolm.2018.11.013>
- Haftenberger, M., Laußmann, D., Ellert, U., Kalcklösch, M., Langen, U., Schlaud, M., Schmitz, R., & Thamm, M. (2013). Prevalence of sensitisation to aeroallergens and food allergens: Results of the German Health Interview and Examination Survey for Adults (DEGS1). *Bundesgesundheitsblatt – Gesundheitsforschung – Gesundheitsschutz*, 56(5–6), 687–697. <https://doi.org/10.1007/s00103-012-1658-1>
- Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J., & Zimmermann, N. E. (2013). Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, 3(3), 203–207. <https://doi.org/10.1038/nclimate1687>
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2017). *dismo: Species distribution modeling. R package version 1.1-4*. <https://CRAN.R-project.org/package=dismo>
- Hirst, J. M. (1952). An automatic volumetric spore trap. *Annals of Applied Biology*, 39(2), 257–265. <https://doi.org/10.1111/j.1744-7348.1952.tb00904.x>
- Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., & Velling, P. (2010). Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. *Forestry*, 83(1), 103–119. <https://doi.org/10.1093/forestry/cpp035>
- IPCC. (2014). *Climate change 2014: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change* [V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova,

- B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (eds.)). Cambridge University Press, IPCC.
- Kim, K. R., Oh, J.-W., Woo, S.-Y., Seo, Y. A., Choi, Y.-J., Kim, H. S., Lee, W. Y., & Kim, B.-J. (2018). Does the increase in ambient CO₂ concentration elevate allergy risks posed by oak pollen? *International Journal of Biometeorology*, 62(9), 1587–1594. <https://doi.org/10.1007/s00484-018-1558-7>
- Kjellström, E., Nikulin, G., Strandberg, G., Christensen, O., Jacob, D., Keuler, K., Lenderink, G., Meijgaard, E., Schär, C., Somot, S., Sorland, S., Teichmann, C., & Vautard, R. (2018). European climate change at global mean temperature increases of 1.5 and 2°C above pre-industrial conditions as simulated by the EURO-CORDEX regional climate models. *Earth System Dynamics*, 9, 459–478. <https://doi.org/10.5194/esd-9-459-2018>
- Kurganskiy, A., Skjøth, C. A., Baklanov, A., Sofiev, M., Saarto, A., Severova, E., Smyshlyaev, S., & Kaas, E. (2020). Incorporation of pollen data in source maps is vital for pollen dispersion models. *Atmospheric Chemistry and Physics*, 20(4), 2099–2121. <https://doi.org/10.5194/acp-20-2099-2020>
- Leuschner, C., & Ellenberg, H. (2017). *Ecology of Central European forests: Vegetation ecology of Central Europe*. (Vol. I). Springer International Publishing. <https://doi.org/10.1007/978-3-319-43042-3>
- Liaw, A., & Wiener, M. (2002). Classification and regression by RandomForest. *R News*, 2(3), 18–22.
- Lind, T., Ekebohm, A., Alm Kübler, K., Östensson, P., Bellander, T., & Löhmus, M. (2016). Pollen Season Trends (1973–2013) in Stockholm Area, Sweden. *PLoS One*, 11(11), e0166887. <https://doi.org/10.1371/journal.pone.0166887>
- Lugonja, P., Brdar, S., Simović, I., Mimić, G., Palamarchuk, Y., Sofiev, M., & Šikoparija, B. (2019). Integration of in situ and satellite data for top-down mapping of Ambrosia infection level. *Remote Sensing of Environment*, 235, 111455. <https://doi.org/10.1016/j.rse.2019.111455>
- Marchand, L. J., Dox, I., Gričar, J., Prislán, P., Leys, S., Van den Bulcke, J., Fonti, P., Lange, H., Matthysen, E., Peñuelas, J., Zuccarini, P., & Campioli, M. (2020). Inter-individual variability in spring phenology of temperate deciduous trees depends on species, tree size and previous year autumn phenology. *Agricultural and Forest Meteorology*, 290, 108031. <https://doi.org/10.1016/j.agrformet.2020.108031>
- McInnes, R. N., Hemming, D., Burgess, P., Lyndsay, D., Osborne, N. J., Skjøth, C. A., Thomas, S., & Vardoulakis, S. (2017). Mapping allergenic pollen vegetation in UK to study environmental exposure and human health. *Science of the Total Environment*, 599–600, 483–499. <https://doi.org/10.1016/j.scitotenv.2017.04.136>
- Mendoza, M., & Araújo, M. B. (2019). Climate shapes mammal community trophic structures and humans simplify them. *Nature Communications*, 10(1), 5197. <https://doi.org/10.1038/s41467-019-12995-9>
- Menzel, A., Ghasemifard, H., Yuan, Y., & Estrella, N. (2021). A first pre-season pollen transport climatology to Bavaria, Germany. *Frontiers in Allergy*, 2. <https://doi.org/10.3389/falgy.2021.627863>
- Morin, X., Fahse, L., Jactel, H., Scherer-Lorenzen, M., García-Valdés, R., & Bugmann, H. (2018). Long-term response of forest productivity to climate change is mostly driven by change in tree species composition. *Scientific Reports*, 8(1), 5627. <https://doi.org/10.1038/s41598-018-23763-y>
- Myking, T., & Heide, O. M. (1995). Dormancy release and chilling requirement of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiology*, 15(11), 697–704. <https://doi.org/10.1093/treephys/15.11.697>
- Noce, S., Collalti, A., & Santini, M. (2017). Likelihood of changes in forest species suitability, distribution, and diversity under future climate: The case of Southern Europe. *Ecology and Evolution*, 7(22), 9358–9375. <https://doi.org/10.1002/ece3.3427>
- Oteros, J., García-Mozo, H., Alcázar, P., Belmonte, J., Bermejo, D., Boi, M., Cariñanos, P., Díaz de la Guardia, C., Fernández-González, D., González-Minero, F., Gutiérrez-Bustillo, A. M., Moreno-Grau, S., Pérez-Badía, R., Rodríguez-Rajo, F. J., Ruíz-Valenzuela, L., Suárez-Pérez, J., Trigo, M. M., Domínguez-Vilches, E., & Galán, C. (2015). A new method for determining the sources of airborne particles. *Journal of Environmental Management*, 155, 212–218. <https://doi.org/10.1016/j.jenvman.2015.03.037>
- Oteros, J., García-Mozo, H., Hervás, C., & Galán, C. (2013). Biometeorological and autoregressive indices for predicting olive pollen intensity. *International Journal of Biometeorology*, 57(2), 307–316. <https://doi.org/10.1007/s00484-012-0555-5>
- Pauling, A., Rotach, M. W., Gehrig, R., & Clot, B. (2012). A method to derive vegetation distribution maps for pollen dispersion models using birch as an example. *International Journal of Biometeorology*, 56(5), 949–958. <https://doi.org/10.1007/s00484-011-0505-7>
- Pecchi, M., Marchi, M., Moriondo, M., Forzieri, G., Ammoniaci, M., Bernetti, I., Bindi, M., & Chirici, G. (2020). Potential impact of climate change on the forest coverage and the spatial distribution of 19 key forest tree species in Italy under RCP4.5 IPCC trajectory for 2050s. *Forests*, 11(9), 934. <https://doi.org/10.3390/f11090934>
- Prasad, A. M., Gardiner, J. D., Iverson, L. R., Matthews, S. N., & Peters, M. (2013). Exploring tree species colonization potentials using a spatially explicit simulation model: Implications for four oaks under climate change. *Global Change Biology*, 19(7), 2196–2208. <https://doi.org/10.1111/gcb.12204>
- Prasad, A., Pedlar, J., Peters, M., McKenney, D., Iverson, L., Matthews, S., & Adams, B. (2020). Combining US and Canadian forest inventories to assess habitat suitability and migration potential of 25 tree species under climate change. *Diversity and Distributions*, 26(9), 1142–1159. <https://doi.org/10.1111/ddi.13078>
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuarema, J. C., Kc, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., ... Tavoni, M. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, 42, 153–168. <https://doi.org/10.1016/j.gloenvcha.2016.05.009>
- Ribeiro, E. C., Batjes, N. H., & Van Oostrum, A. J. M. (2018). *World Soil Information Service (WoSIS) – Towards the standardization and harmonization of world soil data: Procedures Manual 2018*. ISRIC-World Soil Information, 166 pp.
- Ritenberga, O., Sofiev, M., Siljamo, P., Saarto, A., Dahl, A., Ekebohm, A., Sauliene, I., Shalaboda, V., Severova, E., Hoebeke, L., & Ramfjord, H. (2018). A statistical model for predicting the inter-annual variability of birch pollen abundance in Northern and North-Eastern Europe. *Science of the Total Environment*, 615, 228–239. <https://doi.org/10.1016/j.scitotenv.2017.09.061>
- Rojo, J., Orlandi, F., Pérez-Badía, R., Aguilera, F., Ben Dhiab, A., Bouziane, H., Díaz de la Guardia, C., Galán, C., Gutiérrez-Bustillo, A. M., Moreno-Grau, S., Msallem, M., Trigo, M. M., & Fornaciari, M. (2016). Modeling olive pollen intensity in the Mediterranean region through analysis of emission sources. *Science of the Total Environment*, 551–552, 73–82. <https://doi.org/10.1016/j.scitotenv.2016.01.193>
- Rojo, J., Oteros, J., Picornell, A., Ruëff, F., Werchan, B., Werchan, M., Bergmann, K.-C., Schmidt-Weber, C. B., & Buters, J. (2020). Land-use and height of pollen sampling affect pollen exposure in Munich, Germany. *Atmosphere*, 11(2), 145. <https://doi.org/10.3390/atmos11020145>
- Rojo, J., Picornell, A., & Oteros, J. (2019). AeRobiology: The computational tool for biological data in the air. *Methods in Ecology and Evolution*, 10(8), 1371–1376. <https://doi.org/10.1111/2041-210X.13203>
- Rojo, J., Picornell, A., Oteros, J., Werchan, M., Werchan, B., Bergmann, K.-C., Smith, M., Weichenmeier, I., Schmidt-Weber, C. B., & Buters, J. (2021). Consequences of climate change on airborne pollen in

- Bavaria, Central Europe. *Regional Environmental Change*, 21(1), 9. <https://doi.org/10.1007/s10113-020-01729-z>
- Rojo, J., Salido, P., & Pérez-Badia, R. (2015). Flower and pollen production in the Cornicabra olive (*Olea europaea* L.) cultivar and the influence of environmental factors. *Trees*, 29(4), 1235–1245. <https://doi.org/10.1007/s00468-015-1203-6>
- Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T. L., Estrella, N., Seguin, B., Tryjanowski, P., Liu, C., Rawlins, S., & Imeson, A. (2008). Attributing physical and biological impacts to anthropogenic climate change. *Nature*, 453(7193), 353–357. <https://doi.org/10.1038/nature06937>
- Rubio-Cuadrado, Á., Camarero, J. J., del Río, M., Sánchez-González, M., Ruiz-Peinado, R., Bravo-Oviedo, A., Gil, L., & Montes, F. (2018). Long-term impacts of drought on growth and forest dynamics in a temperate beech-oak-birch forest. *Agricultural and Forest Meteorology*, 259, 48–59. <https://doi.org/10.1016/j.agrfor.2018.04.015>
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild. *BioScience*, 52(10), 891–904. [https://doi.org/10.1641/0006-3568\(2002\)052\[0891:THFATL\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2)
- Scherrer, D., D'Amen, M., Fernandes, R. F., Mateo, R. G., & Guisan, A. (2018). How to best threshold and validate stacked species assemblages? Community optimisation might hold the answer. *Methods in Ecology and Evolution*, 9(10), 2155–2166. <https://doi.org/10.1111/2041-210X.13041>
- Schmitz, R., Ellert, U., Kalcklösch, M., Dahm, S., & Thamm, M. (2013). Patterns of sensitization to inhalant and food allergens – Findings from the German Health Interview and Examination Survey for Children and Adolescents. *International Archives of Allergy and Immunology*, 162(3), 263–270. <https://doi.org/10.1159/000353344>
- Skjøth, C. A., Sommer, J., Brandt, J., Hvidberg, M., Geels, C., Hansen, K. M., Hertel, O., Frohn, L. M., & Christensen, J. H. (2008). Copenhagen – A significant source of birch (*Betula*) pollen? *International Journal of Biometeorology*, 52(6), 453. <https://doi.org/10.1007/s00484-007-0139-y>
- Smith, M., Jäger, S., Berger, U., Šikoparija, B., Hallsdóttir, M., Sauliene, I., Bergmann, K.-C., Pashley, C. H., de Weger, L., Majkowska-Wojciechowska, B., Rybniček, O., Thibaudon, M., Gehrig, R., Bonini, M., Yankova, R., Damialis, A., Vokou, D., Gutiérrez Bustillo, A. M., Hoffmann-Sommergruber, K., & van Ree, R. (2014). Geographic and temporal variations in pollen exposure across Europe. *Allergy*, 69(7), 913–923. <https://doi.org/10.1111/all.12419>
- Sofiev, M. (2017). On impact of transport conditions on variability of the seasonal pollen index. *Aerobiologia*, 33(1), 167–179. <https://doi.org/10.1007/s10453-016-9459-x>
- Stagge, J. H., Kingston, D. G., Tallaksen, L. M., & Hannah, D. M. (2017). Observed drought indices show increasing divergence across Europe. *Scientific Reports*, 7(1), 14045. <https://doi.org/10.1038/s41598-017-14283-2>
- Thom, D., Rammer, W., & Seidl, R. (2017). Disturbances catalyze the adaptation of forest ecosystems to changing climate conditions. *Global Change Biology*, 23(1), 269–282. <https://doi.org/10.1111/gcb.13506>
- van Vuuren, D. P., Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G. C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S. J., & Rose, S. K. (2011). The representative concentration pathways: An overview. *Climatic Change*, 109(1–2), 5–31. <https://doi.org/10.1007/s10584-011-0148-z>
- Verstraeten, W. W., Dujardin, S., Hoebeke, L., Bruffaerts, N., Kouznetsov, R., Dendoncker, N., Hamdi, R., Linard, C., Hendrickx, M., Sofiev, M., & Delcloo, A. W. (2019). Spatio-temporal monitoring and modelling of birch pollen levels in Belgium. *Aerobiologia*, 35(4), 703–717. <https://doi.org/10.1007/s10453-019-09607-w>
- Wade, T. G., Riitters, K. H., Wickham, J. D., & Jones, K. B. (2003). Distribution and causes of global forest fragmentation. *Conservation Ecology*, 7(2). <https://doi.org/10.5751/ES-00530-070207>
- Wan, J.-Z., Wang, C.-J., & Yu, F.-H. (2018). Human footprint and climate disappearance in vulnerable ecoregions of protected areas. *Global and Planetary Change*, 170, 260–268. <https://doi.org/10.1016/j.gloplacha.2018.09.002>
- Wang, N., McAllister, H. A., Bartlett, P. R., & Buggs, R. J. A. (2016). Molecular phylogeny and genome size evolution of the genus *Betula* (Betulaceae). *Annals of Botany*, 117(6), 1023–1035. <https://doi.org/10.1093/aob/mcw048>
- Wildlife Conservation Society-WCS, & Center For International Earth Science Information Network-CIESIN-Columbia University. (2005). *Last of the Wild Project, version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic)*. NASA Socioeconomic Data and Applications Center (SEDAC). <https://doi.org/10.7927/H4M61H5F>
- Working Group on Coupled Modelling. (2011). *The WCRP Coupled Model Intercomparison Project—Phase 5 (CMIP5)—CLIVAR Exchanges Special Issue: Vol. No. 56, Vol 16*.
- Xu, C., Gertner, G. Z., & Scheller, R. M. (2007). Potential effects of interaction between CO₂ and temperature on forest landscape response to global warming. *Global Change Biology*, 13(7), 1469–1483. <https://doi.org/10.1111/j.1365-2486.2007.01387.x>
- Zhang, C., Chen, Y., Xu, B., Xue, Y., & Ren, Y. (2020). Improving prediction of rare species' distribution from community data. *Scientific Reports*, 10(1), 12230. <https://doi.org/10.1038/s41598-020-69157-x>
- Zhang, Y., Bielory, L., Mi, Z., Cai, T., Robock, A., & Georgopoulos, P. (2015). Allergic pollen season variations in the past two decades under changing climate in the United States. *Global Change Biology*, 21(4), 1581–1589. <https://doi.org/10.1111/gcb.12755>
- Ziello, C., Sparks, T. H., Estrella, N., Belmonte, J., Bergmann, K. C., Bucher, E., Brighetti, M. A., Damialis, A., Detandt, M., Galán, C., Gehrig, R., Grewling, L., Gutiérrez Bustillo, A. M., Hallsdóttir, M., Kockhans-Bieda, M.-C., De Linares, C., Myszkowska, D., Páldy, A., Sánchez, A., ... Menzel, A. (2012). Changes to airborne pollen counts across Europe. *PLoS One*, 7(4), e34076. <https://doi.org/10.1371/journal.pone.0034076>
- Ziska, L. H., & Beggs, P. J. (2012). Anthropogenic climate change and allergen exposure: The role of plant biology. *Journal of Allergy and Clinical Immunology*, 129(1), 27–32. <https://doi.org/10.1016/j.jaci.2011.10.032>
- Ziska, L. H., Makra, L., Harry, S. K., Bruffaerts, N., Hendrickx, M., Coates, F., Saarto, A., Thibaudon, M., Oliver, G., Damialis, A., Charalampopoulos, A., Vokou, D., Heidmarsson, S., Gudjohnsen, E., Bonini, M., Oh, J.-W., Sullivan, K., Ford, L., Brooks, G. D., ... Crimmins, A. R. (2019). Temperature-related changes in airborne allergenic pollen abundance and seasonality across the northern hemisphere: A retrospective data analysis. *The Lancet Planetary Health*, 3(3), e124–e131. [https://doi.org/10.1016/S2542-5196\(19\)30015-4](https://doi.org/10.1016/S2542-5196(19)30015-4)

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Rojo, J., Oteros, J., Picornell, A., Maya-Manzano, J. M., Damialis, A., Zink, K., Werchan, M., Werchan, B., Smith, M., Menzel, A., Timpf, S., Traidl-Hoffmann, C., Bergmann, K.-C., Schmidt-Weber, C. B., & Buters, J. (2021). Effects of future climate change on birch abundance and their pollen load. *Global Change Biology*, 27, 5934–5949. <https://doi.org/10.1111/gcb.15824>