



Disentangling the effects of feedback structure and climate on *Poaceae* annual airborne pollen fluctuations and the possible consequences of climate change



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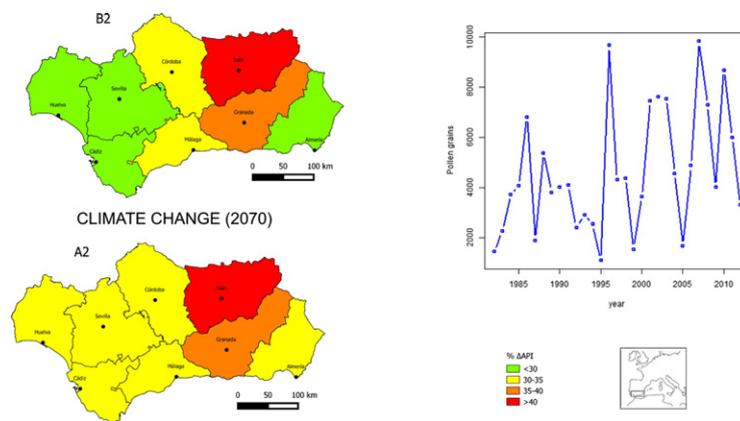
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HIGHLIGHTS

- A novel methodological approach is proposed to study long-term airborne pollen.
- We modelled the long-term airborne *Poaceae* pollen fluctuations.
- Feedback structure and climate drive the *Poaceae* pollen fluctuations.
- Climate change effects on pollen levels were investigated.
- Increase of pollen levels up to 44.3% by 2070 in Southern Spain are predicted.

GRAPHICAL ABSTRACT



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ABSTRACT

Pollen allergies are the most common form of respiratory allergic disease in Europe. Most studies have emphasized the role of environmental processes, as the drivers of airborne pollen fluctuations, implicitly considering pollen production as a random walk. This work shows that internal self-regulating processes of the plants (negative feedback) should be included in pollen dynamic systems in order to give a better explanation of the observed pollen temporal patterns. This article proposes a novel methodological approach based on dynamic systems to investigate the interaction between feedback structure of plant populations and climate in shaping long-term airborne *Poaceae* pollen fluctuations and to quantify the effects of climate change on future airborne pollen concentrations. Long-term historical airborne *Poaceae* pollen data (30 years) from Cordoba city

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(Southern Spain) were analyzed. A set of models, combining feedback structure, temperature and actual evapotranspiration effects on airborne *Poaceae* pollen were built and compared, using a model selection approach. Our results highlight the importance of first-order negative feedback and mean annual maximum temperature in driving airborne *Poaceae* pollen dynamics. The best model was used to predict the effects of climate change under two standardized scenarios representing contrasting temporal patterns of economic development and CO₂ emissions. Our results predict an increase in pollen levels in southern Spain by 2070 ranging from 28.5% to 44.3%. The findings from this study provide a greater understanding of airborne pollen dynamics and how climate change might impact the future evolution of airborne *Poaceae* pollen concentrations and thus the future evolution of related pollen allergies.

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1. Introduction

Pollen allergies are the most common form of seasonal respiratory allergic disease in Europe. Pollen from *Poaceae* species, which are highly allergenic, elicits allergic responses in 35% of the European population (D'Amato et al., 2007; Weger et al., 2013). During the last few decades, the prevalence of pollen allergies has increased in European countries (D'Amato et al., 2007).

The *Poaceae* family is well represented in the Iberian Peninsula and the most abundant genera causing pollinosis are: *Phleum*, *Dactylis*, *Lolium*, *Trisetum*, *Festuca*, *Poa*, *Cynodon* and *Anthoxanthum* (Subiza, 2003). In Spain particularly, these taxa are important causes of pollinosis, although the average percentage of sensitivity to *Poaceae* pollen varies depending on the region (Jato et al., 2009). In Southern Spain, sensitization to *Poaceae* pollen reaches 59% of the population with respiratory allergy (Pereira et al., 2006).

Airborne pollen concentrations fluctuate considerably from year to year. Currently, it has been established that these fluctuations are exclusively governed by exogenous processes, such as temperature and water availability (Dahl et al., 2013; Galán et al., 1995). According to this perspective, airborne pollen fluctuations can be seen as random walk processes with a distribution that becomes wider with time (i.e., its variance is unbounded and there is no correlation with time (Royama, 1992)). A dynamic process with this characteristic implies an unstable system. However, empirical evidence shows that long-term *Poaceae* airborne pollen fluctuations are fairly stable with respect to a trend (or, if not a trend, to its persistent state) and do not deviate or drift away unbounded (García-Mozo et al., 2010a). Therefore, airborne pollen fluctuations could be the consequence of negative feedback mechanisms (internal or endogenous processes), able to persist over time in a state of dynamic equilibrium with their environment (Crone, 2013; Ferrero et al., 2014; Hernández Plaza et al., 2012; Jato et al., 2009; Lima et al., 2012). Understanding how both feedback structure and exogenous factors interact in shaping the dynamic of populations is fundamental to our ability to manage and predict ecosystem response under climate change. In a recent paper, Lima et al. (2012) disentangled the effects of feedback structure and climate in *Descurainia sophia* and *Veronica hederifolia*. While *D. sophia* exhibited a second-order feedback and low climate influence, *V. hederifolia* was characterized by a first-order feedback structure and important effects from temperature and rainfall.

Climate change is one of the greatest threats to future sustainable development given its socioeconomic impacts on many sectors of human activity and it is anticipated to have large impacts on human health (Ziska et al., 2008). A major concern is that the amount of airborne pollen, a primary cause of allergic rhinitis, might increase with climate change, thus increasing the number of people affected (Beggs and Bambrick, 2005; Cecchi et al., 2010). This concern is particularly relevant for the *Poaceae* family which is widely distributed over the Mediterranean area, one of the most prominent hotspots in future climate-change projections (Giorgi and Lionello, 2008).

In this study, we have hypothesized the existence of endogenous processes (negative feedback structures) regulating airborne *Poaceae*

pollen fluctuations. Understanding how endogenous and exogenous processes interact in shaping pollen fluctuations will allow us to forecast more accurately airborne pollen concentrations and to evaluate the effects of climate change (Zhang et al., 2013). More specifically, statistical models combining internal (feedback structure) and external (climate) factors and a 30-year airborne *Poaceae* pollen database have been combined in order to a) examine the structure of long-term airborne pollen fluctuations and b) predict the possible consequences of future climate change in a Mediterranean climate area.

2. Material and methods

2.1. Study site and database

Daily airborne *Poaceae* pollen data from 1982 to 2012 were obtained in Córdoba city (37° 5' N, 4° 45' W; 120 m a.s.l.). This city is situated in the Andalusian region (Southern Spain) bounded in the north by the Sierra Morena mountains, where Mediterranean forests and “dehesas” are the main vegetation, and in the south by the Subbética Mountains, where olive groves predominate. The local climate is Mediterranean with a continental influence, marked by the considerable variation between warm and cold seasons. The average annual temperature and the average cumulative annual precipitation for the period 1971–2000 were 17.8 °C and 621 mm, respectively (AEMET, 2004).

The data set was collected using a Hirst-type volumetric spore trap (Hirst, 1952), following the standard methodology set by the Spanish Aerobiology Network (REA) (Galán et al., 2007) and the Minimum Requirements for the European Aeroallergen Network (EAN) (Galán et al., 2014). Daily pollen concentrations, which peaked in the second week of May, were expressed as the average number of *Poaceae* pollen grains per cubic meter of air. Annual Pollen Index (API) was calculated as the yearly sum of daily pollen concentrations following the methodology suggested by Ziello et al. (2012).

2.2. Weather-related variables

Temperature-related variables are considered to be determinant drivers of airborne pollen fluctuations. Here, we considered annual average temperature (T_{av} , average \pm sd; 12.9 °C \pm 1.2), annual average maximum temperature (T_{mx} , 18.7 °C \pm 1.4) and annual average minimum temperature (T_{mn} , 7.0 °C \pm 1.2) as the exogenous factors influencing the API.

Grass development is positively influenced by soil–water availability (Clary et al., 2004). In this respect, evapotranspiration seems to be a good predictive proxy for water availability (Valencia-Barrera et al., 2002). Therefore, we considered actual evapotranspiration (AET, 406 mm \pm 110) from October 1st to April 30th and computed it from cumulative precipitation and average temperature following Turc's method (Fisher and Pringle, 2013). All weather-related variables were provided by the Spanish Meteorological Agency (AEMET) from a weather station located within 1 km of the monitoring site.

2.3. Statistical models of pollen dynamics

Annual Pollen Index (API) dynamics is the result of the combined effect of two major types of processes. Based on Berryman (1999) we will call exogenous (i.e., external to and no dependent on the system) and endogenous (i.e. internal to and dependent on the system). Exogenous disturbances are often viewed as triggers of system behavior, but the causes are contained within the structure of the system itself and create causal feedback loops.

In order to ensure that the regression was not biased from common trends in the data, we de-trended the API data (i.e., rotated the series around the linear or quadratic trend) (Royama, 1992). Next, we defined the annual rate of API increases as $R_t = \ln(A_t) - \ln(A_{t-1})$ (the first-difference of log-API), where A_t is the de-trended API and A_{t-1} is the same series with a delay of one year.

A model incorporating both internal and external processes may be depicted as $R_t = f(A_{t-d}, Z_{t-d}, \epsilon_t)$, which denotes the number of lags to be included, Z_{t-d} represents the climatic conditions and ϵ_t exhibits random noise. We used the exponential form of the discrete time logistic model, in terms of the annual rates of API increases (Ricker, 1954; Royama, 1992), as our form for the function f to fit the time series data:

$$R_t = r_m - e^{a \cdot \ln(A_{t-d}) + b} \tag{1}$$

where r_m is a constant representing the maximum productive rate observed, and a and b are parameters. For statistical convenience r_m was fixed to 2, a value extracted from raw observed data. This model represents the basic feedback structure and allows for climate variables to be included based on population dynamics theory (Royama, 1992). In this manner, mechanistic hypotheses about the effects of climate on pollen fluctuations can be established to represent perturbations of an exogenous factor Z . To estimate the order of process d (lags), we used Pollard's test (García de León et al., 2014; Pollard et al., 1987).

Eq. (1) was modified to represent independent climate perturbations (exogenous factors) in an additive way (Lima et al., 2012):

$$R_t = r_m - e^{a \cdot \ln(A_{t-d}) + b} + c * \ln(Z_t) \tag{2}$$

where Z_t is the environmental condition (e.g., temperature). Variation in this parameter modifies the equilibrium point and could alter its stability.

Changes in b (Eq. (1)) involve external factors that act non-additively on API:

$$R_t = r_m - e^{a \cdot \ln(A_{t-d}) + b + c \cdot \ln(Z_t)} \tag{3}$$

here, for example, precipitation may influence water availability, affecting the API potential but not its stability.

Finally, exogenous factors may have a complex influence on API dynamics as the nonlinear parameter, a , changes (Eq. (1)) (nonlinear perturbation):

$$R_t = r_m - e^{(a+c \cdot \ln(Z_t)) \cdot \ln(A_{t-d}) + b} \tag{4}$$

in this last case, curvature of the R-function curve and the slope at equilibrium are changed, representing a nonlinear perturbation, changing both the equilibrium point and its stability.

2.4. Model fitting and model selection

We fitted Eqs. (1)–(4) using nonlinear least squares (nls) regressions with the nls library in the software R (R Core Team, 2013). In particular, the models were fitted by minimizing the Akaike criterion (AIC) and maximizing the pseudo R^2 based on the deviance residual (Burham and Anderson, 2002; Freese and Long, 2006; Zhang et al., 2013). The model to be used was chosen on the basis of the goodness-of-fit, the ability to describe the correct dynamics and the appropriateness.

2.5. Climate scenarios

The effects of climate change were assessed with a general circulation model, ECHAM4/OPYC3. This is a fourth-generation atmospheric general circulation model, ECHAM4, coupled with an ocean general circulation model, OPYC3 (Castellanos-Frías et al., 2014). The target years were set to 2020, 2050 and 2070 using two different standardized scenarios. These two scenarios include contrasting temporal patterns of economic development and CO₂ emissions. The A2 scenario describes a world with great regional inequality due to a continuous increase in global population, economic growth and technological change, and medium-high CO₂ emissions. The B2 scenario represents a world with economic, social and environmental sustainability that relies on progressive population growth (lower than in A2), intermediate levels of economic development, slower and more diverse technological changes and low-medium CO₂ emissions. Climate change data used in the model were taken from Ciscar et al. (2011).

2.6. Assessing the effects of climate change on Poaceae airborne pollen fluctuations

In order to assess the effects of climate change, the equilibrium point of the API was mathematically determined for the best model. Next, the model was parameterized with the climatic information for current and future climates (target years) (based on the climate scenarios considered (IPCC, 2007)). The effects of climate change on Poaceae airborne pollen fluctuations were assessed based on the proportion of change of their equilibrium points in relation to the current climate.

Finally, the model was used to estimate the equilibrium population for all the main cities in Andalusia, other than Córdoba, and to extrapolate for the whole Andalusian region. A Welch two samples t-test was conducted to compare predictions under the two contrasting scenarios. All maps were created using the geographic information system, QGIS 2.8.2.

3. Results

3.1. Feedback structure and exogenous perturbations

The numerical fluctuations of the API were characterized by oscillations and a positive trend (Fig. 1.a) (Pearson's test, $r = 0.2$,

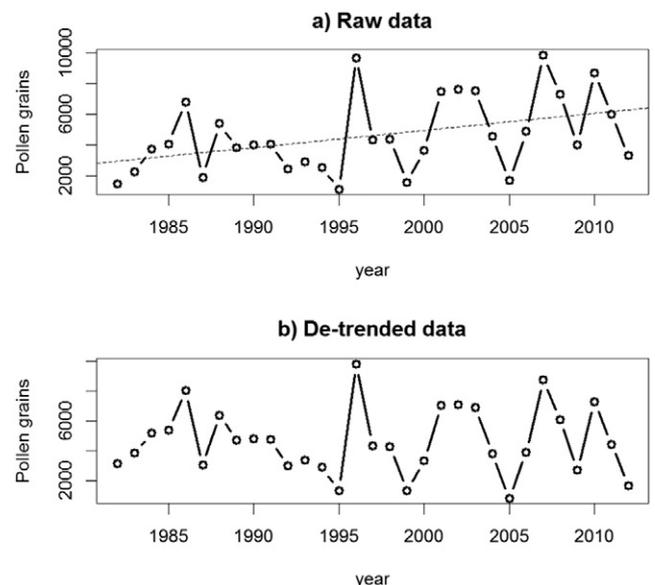


Fig. 1. Variation in pollen grains of Poaceae in Córdoba city (1982–2012): (a) Raw data; dashed line shows trend line; (b) de-trended data.

$p < 0.05$). After de-trending (Fig. 1.b), the annual rate of the API increase (R_t) exhibited a first-order negative feedback structure (Eq. (1)) (Table 1) as the most important component. As a consequence of this stabilizing feedback, pollen fluctuations exhibited stable approaches to equilibrium (regular oscillations).

The pure endogenous model explained 42% of the R_t increases (Model 1, Table 2). Several models selected for evaluating climate impacts on the annual rate of API improved the explained variance of the pure endogenous model by up to 6% (Table 2).

Our results indicate that the API was essentially affected positively by maximum temperature in an additive way (Model 3; Table 2). Models including additive effects of average temperature, minimum temperature and actual evapotranspiration, as well as non-additive and nonlinear effects of minimum temperature (Models 2, 4, 5, 8 and 12, Table 2) did not improve the explanatory capacity of the pure endogenous model (Model 1, Table 2). Other models including non-additive and nonlinear effects on average temperature, maximum temperature and actual evapotranspiration (Models 6, 7, 9, 10, 11 and 13, Table 2) improved the pure endogenous model slightly, up to 2% of its variance.

3.2. Effects of climate change

The equilibrium point (A^*) of the best model (Model 3, Table 2) was estimated as:

$$A^* = e^{\frac{1}{\alpha}(\ln[r_m + c \cdot \ln(T_{mx})] - b)} \quad (5)$$

Eq. (5) was used to compute the projected scenarios in order to compare them to the current climate (baseline) using the following expression:

$$\% \Delta A^* = \left(\frac{A_{\text{scenario}}^* - A_{\text{current}}^*}{A_{\text{current}}^*} \right) * 100. \quad (6)$$

Results showed a continuous increase in pollen levels in Córdoba in the next decades (Table 3), reaching cumulative rises of 30.1 and 31.8% by 2070 under B2 and A2 scenarios, respectively (Table 3). Extrapolations made for the remaining chief cities in Andalusia showed a similar tendency (Table 3). Under the moderate B2 scenario, predicted equilibrium API changes ranged between 28.5% (Sevilla) and 40.3% (Jaén) by 2070 (Table 3; Fig. 2). Under the severe A2 scenario, these changes ranged between 31.3% (Sevilla) and 44.3% (Jaén) (Table 3; Fig. 2). There were no significant differences in the predictions between either scenarios (Welch two samples t-test, $t = -0.82$, $p = 0.42$).

4. Discussion

4.1. Feedback structure and perturbations

This study brings to light the first evidence that airborne pollen fluctuations are regulated not only by climate factors but also by endogenous ones. Our long-term analysis showed that both endogenous and exogenous processes are key factors for determining *Poaceae* airborne pollen fluctuations. A nonlinear first-order negative feedback structure captured the essential elements of API dynamics and indicated the existence of rapid negative feedback. Although most aerobiological literature (Aboulaich et al., 2009, 2013; Cariñanos et al., 2014;

García-Mozo et al., 2009) establishes exogenous factors as being exclusive drivers when explaining pollen dynamics, our results suggest that the endogenous feedback structure of the system should also be considered in order to fully understand pollen fluctuations. This is supported by Jato et al. (2009), who concluded that weather-related factors alone are insufficient in accounting for *Poaceae* pollen fluctuations and Crone (2013), who suggested that endogenous processes may also be more important for *Poaceae* pollen dynamics than previously assumed, due to the impact of the intrinsic growth rhythm on flowering time.

Poaceae development is influenced by exogenous perturbations, mainly temperature and rainfall. These exogenous variables improved the explained variance of the pure endogenous models by up to 6% (Table 2). We found maximum temperature (T_{mx}) to be the most important exogenous variable (Model 3; Table 2). This finding is in line with Rodríguez-Rajo et al. (2003) who reported that pollen concentrations of *Poaceae* are highly correlated with maximum temperature. Maximum temperature affected API mainly in an additive way but in non-additive and nonlinear ways as well (Models 7 and 11; Table 2). However, the effects of temperature and precipitation on *Poaceae* development must be interpreted with caution. Recent studies such as Zhang et al. (2014) and Zhang et al. (2015) claim that these effects may be confused with air pollutants (e.g. ozone), carbon dioxide, other greenhouse gases, cloud coverage and sunshine hours. Special caution must be exercised in the climate context because several of these confounding variables are predicted to change in parallel with temperature and rainfall.

Recent studies assume that the effect of average temperature is additive and accounted for by linear models. Our results did not confirm this assumption (Model 2, Table 2), rather, they are in agreement those of Ziello et al. (2012) who, in a transnational study, did not find a linear relationship between API and the mean temperature in *Poaceae* pollen. Otherwise, we found a weak non-additive and nonlinear relationship between average temperature and API.

The influence of minimum temperature on *Poaceae* pollen levels has been described by some authors (e.g. Recio et al., 2010). Our results indicate that the API was uninfluenced by minimum temperature. A possible explanation could be the different time periods considered to establish the minimum temperature; the whole year in this paper while only the period between March and April in the cited reference.

Linear response of the API to temperature, as generally suggested in the literature (e.g. Recio et al., 2010), seems insufficient in accounting for *Poaceae* pollen fluctuations (Jato et al., 2009). In general, our results suggest that the API responds to temperature in a complex way. Therefore, small changes in temperature could exert big changes in the API because of the nonlinear response. This general finding could be crucial to API forecasting, because ignoring it could lead to oversized predictions of pollen production.

In our study, actual evapotranspiration was not a major abiotic factor and it presented a little effect on API fluctuations (Table 3). This is surprising because other authors (Clary et al., 2004; García-Mozo et al., 2010b) have found water availability to be very important for the development of *Poaceae*, especially in Mediterranean areas, finding a strong relationship between floral intensity and rainfall. We suggest two possible explanations for the weak effect of actual evapotranspiration. First, delayed effects of evapotranspiration on R_t exist and were not considered. We tested it using Eq. (1) but no delayed effects were found (results not shown). Second, the studied pollen population represents a mixture of perennial and annual grasses, although pollen production from perennial species may dominate. Most perennial Mediterranean species clearly optimize carbon assimilation with a tight regulation of their stoma conductance. A tight regulation of stoma conductance in perennial *Poaceae* may weaken water availability dependence to the point where temperature hinders its effect. This is supported by León-Ruiz et al. (2011) who determined that perennial *Poaceae* produce disproportionately high pollen amounts relative to annual *Poaceae*. Further support is provided by Clary et al. (2004) who found that the

Table 1
Results of Pollard's test at different time lags.

Lag	R	P
1	-0.6	<0.01
2	-0.19	0.72

Table 2

Models of Annual Pollen Index (API) dynamics: R_t = natural logarithmic per capita growth rate between years t and $t - 1$; r_m = maximum log per capita growth rate; a , b and c are constants. T_{av} = average temperature; T_{mx} = average of maximum temperatures; T_{mn} = average of minimum temperatures; AET = actual evapotranspiration; AIC_c = corrected Akaike information criterion; ΔAIC_c = difference between AIC_c and the lowest AIC_c ; w = Akaike weight; pR^2 = Efron's pseudo correlation coefficient. Climate variables were computed from October 1st to April 30th: The best model is represented in bold.

Model	r_m	A	B	c	AIC_c	ΔAIC_c	W	pR^2
1) $R_t = r_m - e^{a + \ln(A_t - 1) + b}$	2	0.5	-3.3	-	61.8	1.1	0.14	0.42
2) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(T_{av})$	2	0.3	-1.87	0.3	63.4	3.1	0.05	0.42
3) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(T_{mx})$	2	0.1	0.91	1.8	60.7	0.0	0.25	0.48
4) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(T_{mn})$	2	0.4	-2.2	0.3	63.8	3.1	0.05	0.42
5) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(AET)$	2	0.4	-2.1	0.1	64.0	3.3	0.05	0.42
6) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(T_{av})$	2	0.4	-4.1	0.4	63.6	3.0	0.05	0.43
7) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(T_{mx})$	2	0.4	-1.3	-0.6	63.0	2.4	0.07	0.44
8) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(T_{mn})$	2	0.5	-3.3	0.1	64.1	3.4	0.04	0.42
9) $R_t = r_m - e^{a + \ln(A_t - 1) + b} + c * \ln(AET)$	2	0.4	-4.4	0.3	63.2	2.5	0.07	0.44
10) $R_t = r_m - e^{((a+c*\ln(T_{av}))+\ln(A_{t-1}))+b)}$	2	0.3	-3.1	0.1	63.6	3.0	0.06	0.43
11) $R_t = r_m - e^{((a+c*\ln(T_{mx}))+\ln(A_{t-1}))+b)}$	2	0.7	-3.1	-0.1	63.2	2.5	0.07	0.44
12) $R_t = r_m - e^{((a+c*\ln(T_{mn}))+\ln(A_{t-1}))+b)}$	2	0.5	-3.2	0.01	64.1	3.4	0.05	0.42
13) $R_t = r_m - e^{((a+c*\ln(AET))+\ln(A_{t-1}))+b)}$	2	0.2	-2.6	0.03	64.5	3.8	0.04	0.43

perennial *Poaceae Brachypodium retusum* Pers. (Beauv.) exhibits a low dependence on water availability due to a tight regulation of its stoma opening.

4.2. Effects of climate change

According to all the models assessed by the IPCC, temperature is anticipated to increase and rainfall to decrease in the Mediterranean basin. Therefore, climate change is expected to cause an increase in *Poaceae* pollen production (Emberlin et al., 1994; García-Mozo et al., 2011). Our results confirm such a rise and predict an increase in API in southern Spain by 2070 above 28% and 30% under the moderate (B2) and extreme (A2) scenarios, respectively (Table 3).

There did not seem to be any different patterns associated with the climate model used. Nevertheless, large differences were observed at the province level (Table 3). Jaén and Granada were the provinces with the highest predicted climate change impacts. These provinces are located inland in eastern Andalusia, where the climate is Median-Mediterranean and the inland positioning leads to a larger range of temperatures, with colder winters and warmer summers than coastal regions.

Larger temperature ranges, with low minimum temperatures due to continental positioning may strengthen the role of maximum temperature in the early months of the growing season. Conversely, smaller temperature ranges due to coastal positioning (Almería, Cádiz, Huelva and Málaga) and the influence of the Guadalquivir Valley (Sevilla) may moderate the effects of climate change on *Poaceae* pollen

equilibrium densities. These results are in line with the findings of García-Mozo et al. (2011) who reported that maximum increases in *Poaceae* pollen indices will occur in Jaén and Granada and minimum increases will occur in Sevilla and coastal areas due to differing thermal oscillations. Results shown for Andalusia, other than Córdoba, were obtained by extrapolation and should be interpreted with caution. However, they can provide a representation of the likely evolution of pollen allergies in southern Spain.

An increased pollen index due to climate change, as suggested in the present study, will have an impact on *Poaceae* allergies. The clinical consequences of the findings presented in this study are clear: *Poaceae* allergy sufferers will be exposed to higher amounts of airborne pollen in the future, perhaps having negative effects on their daily quality of life (Deak et al., 2013). Additionally, Dapul-Hidalgo and Bielory (2012) stated that an increase in allergen exposure and long distant transport of anemophilous allergenic pollens will generate increases of symptoms of allergies to various species not commonly present in sufficient quantities to cause them. However, the evidence on how climate change will affect aeroallergens is limited as is supported by Dapul-Hidalgo and Bielory (2012) who call attention to studies being focused on limited variables and which are rarely designed to encompass the broad subject of weather, aeroallergens and complex gene–environment interaction in the individuals predisposed to atopic disorders.

The use of this new analytical approach allows for a framework in line with Zhang et al. (2013), in which exogenous and endogenous factors can be combined to bring a greater understanding of airborne pollen fluctuations and how climate change might impact the future

Table 3

Andalusian chief cities – baseline maximum temperature and projected shifts (IPCC) by 2020, 2050 and 2070 under the two climate change scenarios considered.

City	Córdoba	Sevilla	Jaén	Granada	Huelva	Cádiz	Almería	Málaga
Latitude N	37° 50'	37° 23'	36° 46'	37° 11'	37° 16'	36° 32'	36° 50'	35° 47'
Longitude W	4° 45'	5° 59'	3° 47'	3° 35'	6° 57'	6° 18'	2° 28'	4° 19'
Baseline maximum temperature (T_{mx} °C) ^a	19.1	20.0	16.4	17.2	19.6	19.6	19.6	19.3
T_{mx} estimated 2020 (B2 scenario)	19.5	20.4	16.8	17.6	20.0	20.0	20.0	19.7
T_{mx} estimated 2020 (A2 scenario)	19.5	20.4	16.8	17.6	20.0	20.0	20.0	19.7
T_{mx} estimated 2050 (B2 scenario)	20.6	21.5	17.9	18.7	21.1	21.1	21.1	20.8
T_{mx} estimated 2050 (A2 scenario)	20.7	21.6	18.0	18.8	21.2	21.2	21.2	20.9
T_{mx} estimated 2070 (B2 scenario)	21.3	22.2	18.6	19.4	21.8	21.8	21.8	21.5
T_{mx} estimated 2070 (A2 scenario)	21.5	22.4	18.8	19.6	22.0	22.0	22.0	21.7
% pollen increase (B2 scenario 2020)	5.1	4.8	6.2	6.0	5.1	5.1	5.1	5.7
% pollen increase (A2 scenario 2020)	5.2	4.9	6.3	6.1	5.1	5.1	5.1	5.8
% pollen increase (B2 scenario 2050)	20.0	18.8	24.4	22.9	19.3	19.3	19.3	19.7
% pollen increase (A2 scenario 2050)	21.7	20.4	26.5	24.9	21.0	21.0	21.0	21.4
% pollen increase (B2 scenario 2070)	30.1	28.5	40.3	35.0	29.3	29.3	29.3	29.9
% pollen increase (A2 scenario 2070)	31.8	31.3	44.3	38.4	32.2	32.2	32.2	32.8

^a Source: Spanish Meteorological Agency (AEMET). Period of reference: 1971–2000.

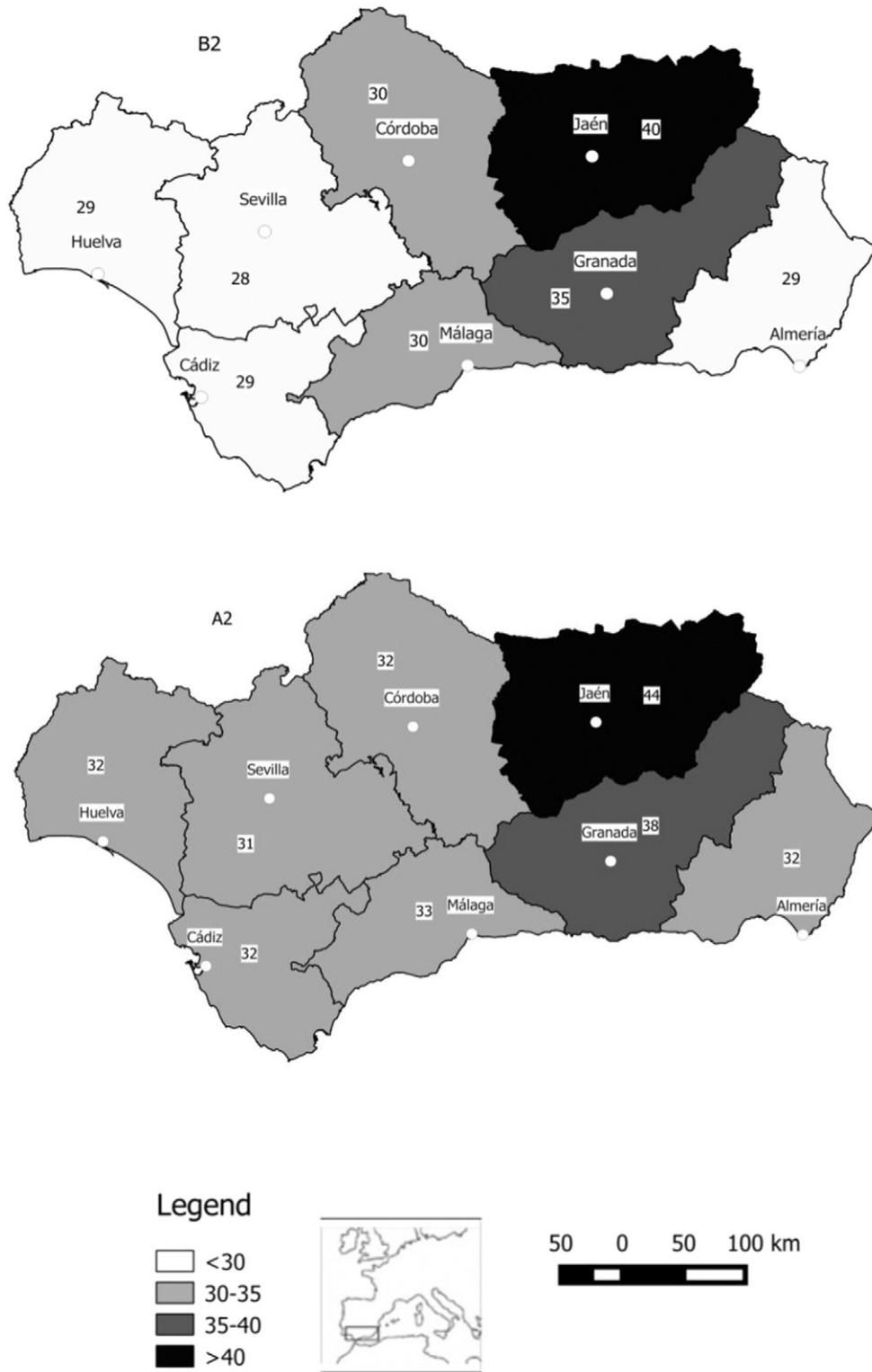


Fig. 2. Maps of forecasted increased equilibrium densities (2070) for airborne *Poaceae* pollen under B2 and A2 scenarios in percentage increase in the *Annual Pollen Index* (% Δ API*) according to Eq. (6).

evolution of pollen levels and, therefore, the future progress of pollen allergies. In particular, we suggest that approaches which ignore the endogenous structure fail to capture underlying phenomena and overestimate future increases in airborne *Poaceae* pollen density. In our work we have only considered some exogenous factors that influence pollen dynamics; other factors, such as land-use, air pollutants or greenhouse gases can also play a relevant role. These variables can be easily incorporated into the proposed framework.

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