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# Charting trends in the evolution of the La Alhambra forest (Granada, Spain) through analysis of pollen-emission dynamics over time

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**Abstract** Changing climate conditions are having an appreciable impact both on the adaptive response of the species growing in urban and peri-urban forests (UPF) and on their evolutionary dynamics. This study sought to chart the evolution and pollen dynamics of major species growing in the La Alhambra peri-urban forest (Granada, Spain) over the last 22 years, to examine correlations with weather-related parameters and to estimate potential trends in the event of future climate change. Findings showed that overall pollen levels have gradually increased over the study period, reflecting both plant species diversification and the ability of Mediterranean species—particularly *Pinus* and *Quercus*—to adapt to short-term water stress situations. Nevertheless, the climate conditions expected over the coming years in the Mediterranean region, with considerable increase in winter temperatures and a drop in precipitation by up to 24 % for summer rainfall, there is likely to be a reduction in the intensity of pollen emissions, at least from species with strict environmental requirements. The results confirm that pollen emission is a valuable biological indicator for estimating the adaptive response of various species and the resilience of the forest mass to climate-change events.

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## 1 Introduction

Urban and peri-urban forests (UPFs) are areas of ecological, landscape and cultural interest located within, or in close proximity to, urban settlements. In these areas, urban and rural activities are juxtaposed, and landscape features are subject to rapid change induced by anthropogenic activity (Douglas 2006). UPFs also play a key role in the quality of city life, providing a range of environmental, recreational, cultural, societal, educational, economic and development benefits and services (Pardo de Donlebún 2012).

Regardless of their origin, the dynamics and biodiversity of these forests vary over time, in response to the different factors affecting them, be they natural or anthropogenic, biotic or abiotic. In recent years, climate change has been one of the factors most affecting UPFs; in addition to prompting a direct response from species and communities (Hansen et al. 2001), climate change entails a number of associated effects including invasion by highly-adaptable colonising species, greater vulnerability to pests and diseases, and greater exposure to extreme weather events such as droughts, floods, hurricanes and snowstorms (Dale et al. 2001). In this context, there is a clear need for indicators that will enable us to chart the response of plant species to a range of environmental stress situations, as well as gauge their resilience, i.e. their ability to attenuate as far as possible the impact of future events (MacIver and Wheaton 2005).

The amount of pollen released by vascular plants during pollination is an indicator of their reproductive status and of the environmental conditions in which they grow (Cariñanos et al. 2004). Analysis of the pollen records for a given area over a number of years reveals the effects of changing weather conditions on the habitual phenological dynamics of species, and on their aerobiological behaviour (Damialis et al. 2007). In the case of urban and peri-urban forests, analysis can highlight changes in the relative contributions of component species, and determine both their response to changing environmental conditions (Cariñanos et al. 2015; Linderholm 2006) and their ability to adapt to new climate scenarios (García-Mozo et al., 2006; Lu et al. 2006).

The aim of this study was to chart the evolution of the La Alhambra peri-urban forest (Granada, Spain) by analysing pollen dynamics over the last 22 years, to identify any changes in species composition, and to examine correlations with weather-related parameters. At the same time, the study sought to evaluate the resilience of component species to water stress situations, and their potential response to future projected climatic change.

## 2 Material and methods

### 2.1 Study area - vegetation inventory

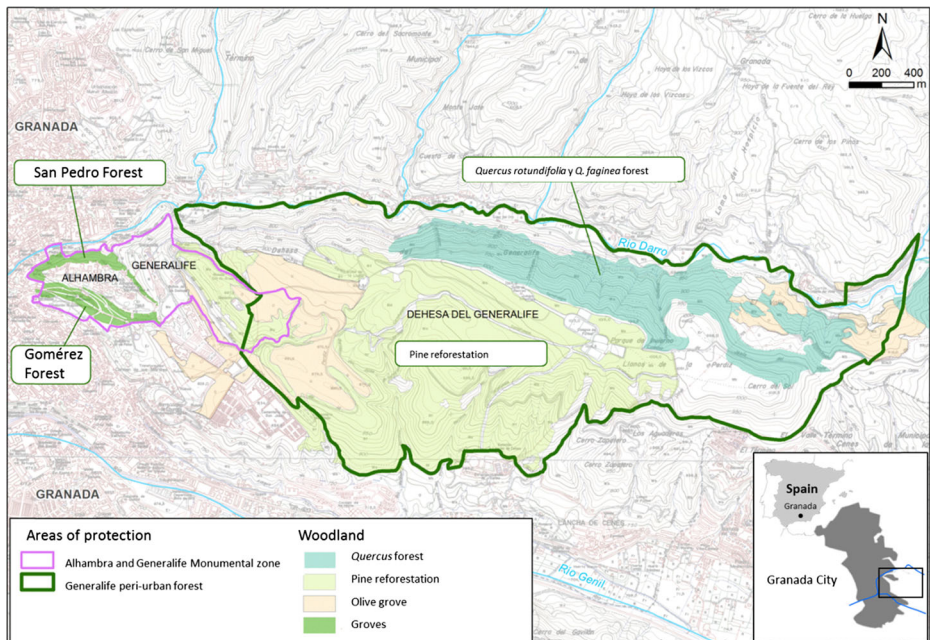
The study was carried out in the forests surrounding the Alhambra, a thirteenth-century Moorish monumental complex in the city of Granada (37° 10'N, 3° 35'W). The complex—comprising the extensive palace buildings themselves and the gardens, cropland and forests surrounding them—is among Spain's most popular tourist attractions, receiving over two and a half million visitors a year, according to official published data on tourist activity in the Alhambra complex (Data of the Tourist, Educative and Cultural Activity in the Monument of la Alhambra and Generalife 2013). The dryland areas of this open secondary anthropogenic forest are similar to sclerophyllous forest, whilst irrigated areas resemble Mediterranean riparian formations (Hagen and De la Cruz Márquez 2010). According to data provided by the Palace Gardens, Forest and Orchards Service, the forest contains over 3000 large trees (diameter at

breast height, DBH > 20 cm), with a mean overall density of 320 trees/ha.; around 40 species are present, distributed over three geographical areas (Fig. 1): the San Pedro forest (5 ha., 900 large trees, 18 species, North Area), the Gómez forest (7 ha., 2000 large trees, 24 species, South area), and the peri-urban Generalife Dehesa, (206 ha., mixed *Pinus* and *Quercus* meso- and supramediterranean series forest, West area) (Perea et al. 2001). The characteristics and species composition of each area are shown in Online Resource 1. The most widespread species is *Celtis australis*, with over one thousand specimens, followed by a slightly smaller abundance of *Ligustrum lucidum*, *Aesculus hippocastanum*, *Platanus x hybrida* and various *Acer* species.

Forest conservation and restoration measures include extensive replacement of elms affected by an outbreak of Dutch Elm disease (*Ophiostoma* sp.) in the 1990s, and the gradual diversification of tree species, involving the annual introduction of 200 specimens of different species under the Alhambra Woodland Restoration programme (2007–2015) implemented by the Alhambra Management Board (Villafranca Jiménez and Salmerón Escobar 2010).

## 2.2 Pollen emissions

Pollen counts were provided by the University of Granada Aerobiological Monitoring Unit, located in the Science Faculty (37° 11'N, 3° 57'W; 685 m a.s.l.). Airborne pollen sampling was carried out in accordance with the standardised Spanish Aerobiology Network procedure (Galán et al. 2007, [http://www.uco.es/rea/infor\\_rea/manual\\_eng.pdf](http://www.uco.es/rea/infor_rea/manual_eng.pdf)), using Hirst-type volumetric suction samplers with a suction rate of 10 l/min. Daily counts, expressed as pollen grains/m<sup>3</sup> of air/day, were analysed for the most widespread anemophilous tree species growing both in the forest (*Acer*, *Ulmus*, *Pinus*, *Quercus*, *Corylus*) and in surrounding areas



**Fig. 1** Location of the three areas forming the Alhambra forest, (Granada, Spain)

(*Cupressus* in the Albayzin district) for the period 1992–2013. The timing of the annual pollen season for each pollen type was calculated using mean daily data for the period under study. For each taxon and study year, the following phenological and aerobiological parameters were calculated: Pollen Index (annual sum of daily values), pollen-season start date (i.e. the date from which 1 pollen grain/m<sup>3</sup>/day was recorded for at least 5 consecutive days, and pollen-season duration (expressed as number of days) (Galán et al. 2001).

### 2.3 Weather data

Weather data were supplied by the Spanish Meteorological Agency (AEMET), from the weather station located at La Cartuja, north of the city of Granada and at same height above sea level (780 m a.s.l.). Seasonal and monthly maximum and minimum temperatures and total seasonal and monthly rainfall for the period 1992–2013 were used to chart changes in airborne pollen data under varying climate conditions.

### 2.4 Statistics

In order to analyse pollen-season trends, the phenological and aerobiological parameters (Pollen Index, PI; Start Date, SD; and Length of Season, LS), were fitted to simple linear regression models. Trends in seasonal maximum and minimum temperatures and seasonal rainfall patterns over the study period were also analysed. To ascertain the impact of weather-related parameters on pollen counts for different species over time, Spearman's non-parametric correlation test was applied for the main monthly weather- and pollen-related parameters. Finally, stepwise multiple regression was performed to identify the parameters most influencing airborne pollen counts. All statistical analyses were carried out using the IBM SPSS 20.0 statistical software package.

## 3 Results

Trends in total airborne pollen counts in Granada during the period 1992–2013 and in pollen counts for the selected anemophilous species in the Alhambra forests over the same period displayed a significant correlation (.829,  $p < 0.01$ ), with peaks and dips in the Pollen Index (PI) occurring at similar times and an overall rising trend in counts over the period as a whole (Online Resource 2). In both cases, the PI rose by over 1000 pollen grains per year.

Analysis of mean daily pollen counts for each taxon over the study period (Online Resource 3) enabled the timing of pollen emission to be identified. Findings confirmed that *Acer*, *Ulmus* and *Corylus* are winter-flowering genera, given their deciduous nature, while *Pinus* and *Quercus* flower in spring and display a prolonged flowering period, lasting until summer, due to the successive flowering of different species growing in the forests: *Pinus halepensis*, *P. pinaster* and *P. sylvestris*; and *Quercus ilex subsp. Rotundifolia* and *Q. faginea*. Data for *Cupressus* pollen counts included pollen emitted not only by species of this genus (*C. sempervirens*, *C. macrocarpa*, *C. arizonica*, *C. lusitanica*), but also by other members of the Cupressaceae (*Juniperus*, *Platycladus*, *Chamaecyparis*), both natural and ornamental, sharing the same pollen morphology. This led to a prolonged airborne pollen presence, lasting from autumn through to the following spring. Mean daily counts for each taxon varied considerably, ranging from very low values of barely 1 pollen grain/day for *Corylus* to the

very high counts of over 500 grains/day recorded for *Cupressus* on several occasions during the flowering period.

Trends for Pollen Index (PI), Start Date (SD) and Length of Season (LS) were analysed in the light of weather data using a simple linear regression model. For PI, only *Cupressus* recorded a significant positive trend, increasing by almost 1000 pollen grains per year (Table 1). A non-significant rising trend was also noted for all other taxa except *Ulmus*. The only noteworthy finding for other parameters was a significant trend towards longer flowering periods for *Pinus* and *Cupressus*.

Analysis of seasonal weather data (maximum and minimum temperature, and rainfall) revealed a slight significant falling trend for maximum winter temperatures (Fig. 2a); negative, though non-significant, trends were also recorded in autumn and winter minimum temperatures (Fig. 2b). Interestingly, temperature rises were most marked in summer (0.06 °C per year for maxima and 0.04 °C for minima), thus reflecting recent trends reported by the IPCC in the Iberian Peninsula (Kovats et al. 2014). Analysis of the seasonal rainfall trends highlighted a decline in spring rainfall, but a significant increase in winter precipitation; no significant change was observed for autumn rainfall (Fig. 2c). The increasing frequency of torrential rains, noted here, is among the major long-term trends reported for the Mediterranean Region (Kovats et al. 2014). It should be noted that, in the analysis of total annual rainfall, several years were classed as severe-drought years, with total rainfall values far below the annual mean of 357 mm for the area (EEA, 2012).

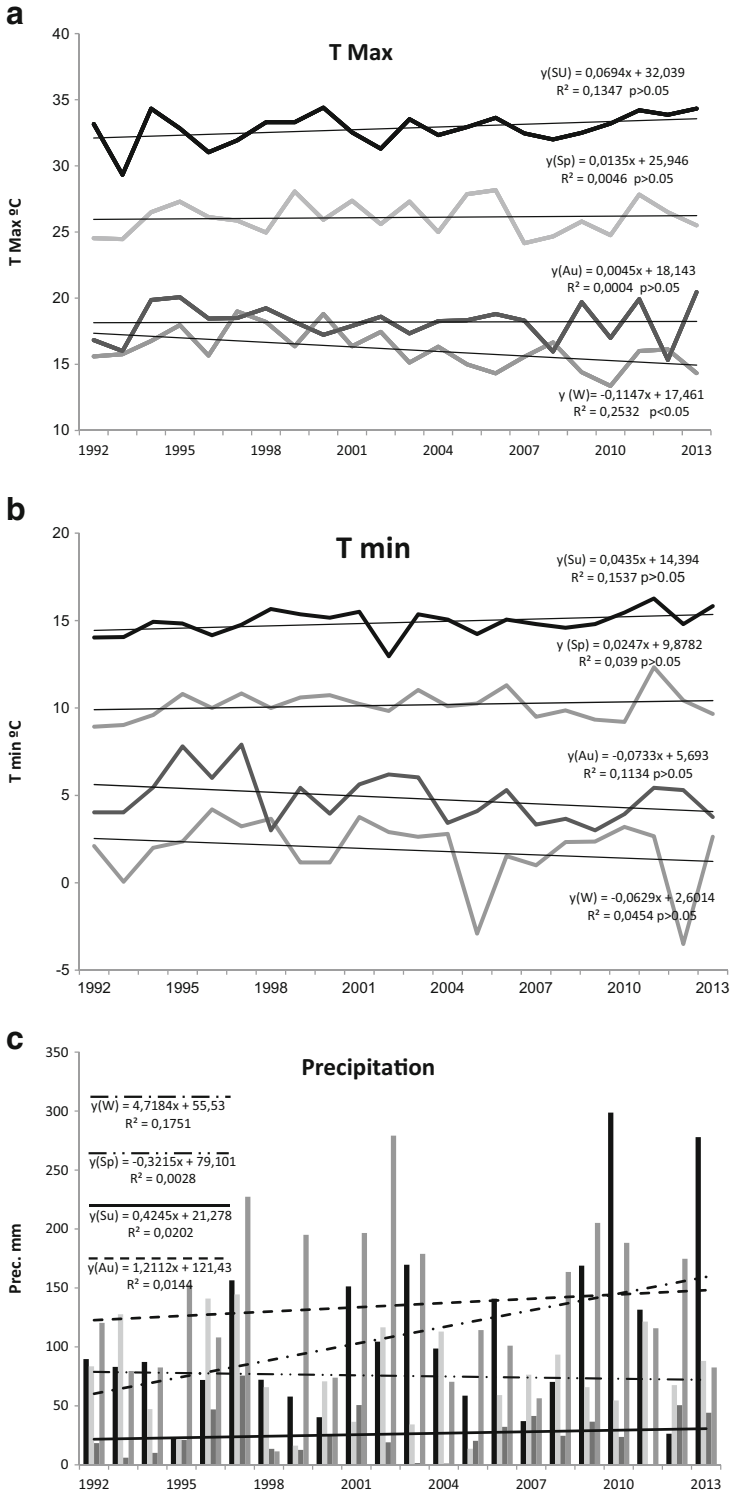
Correlations between monthly weather-related data and pollen-related data showed that *Ulmus* PI was the most dependent on seasonal weather patterns, displaying a significant correlation ( $p < 0.05$ ) with October rainfall and with maximum temperatures in December and February (Table 2). A significant negative correlation was observed between February maximum temperatures and pollen-season start date for *Acer*, *Pinus* and *Quercus*; a significant correlation was also found between length of season and minimum February temperatures for *Acer* and *Pinus*. For *Cupressus*, winter parameters showed the strongest correlation with pollen data: November rainfall with IP; November minimum temperature with pollen-season length, and rainfall in November, December and January with pollen-season start date (SD).

Multiple stepwise regression, taking PI as the dependent variable and monthly weather data both over the months prior to flowering and from flowering onset until the peak annual count, revealed highly-variable behaviour, making it impossible to identify a general model (Table 3). In general terms, the weather parameters most influencing winter-flowering species were those

**Table 1** Slope value and significance (p) for the aerobiological parameters Pollen Index (PI), Start Date (SD) and Length of Season (LS) for the taxa studied over the period 1992–2013

	PI		SD		LS	
	Slope	p	Slope	p	Slope	p
<i>Acer</i>	18.52	.41	−0.261	.46	0.76	.15
<i>Ulmus</i>	−6.25	.29	0.36	.17	−0.195	.53
<i>Corylus</i>	0.36	.77	−0.27	.61	−0.32	.46
<i>Pinus</i>	13.82	.39	0.01	.97	<b>2.238</b>	<b>.00</b>
<i>Quercus</i>	60.77	.34	0.526	.11	0.439	.46
<i>Cupressus</i>	<b>953.86</b>	<b>.00</b>	−0.142	0.42	<b>2.287</b>	<b>.01</b>

In bold, significant values at  $p < 0.05$





◀ **Fig. 2** Linear trends for seasonal maximum (a), minimum temperatures (b) and rainfall (c) in the Meteorological station Granada-Airport (Granada, Spain), over the period 1992–2013. *W* Winter; *Sp* Spring; *Su* Summer; *Au* Autumn

recorded for the autumn months prior to flowering, e.g. maximum November temperatures for *Acer*, October rainfall for *Ulmus* and November and January rainfall for *Corylus*. However, these taxa were also influenced by spring rainfall during the flowering period; in the case of *Ulmus*, for example, rainfall parameters accounted for up to 62 % of variance. For perennial species (*Pinus*, *Quercus*), the parameters most influencing PI were those recorded for the winter months, although *Quercus* flowering behaviour was also strongly influenced by minimum temperatures over the period immediately prior to the peak concentration date. Strikingly, no single variable influenced the regression model for *Cupressus*.

## 4 Discussion

The results showed that pollen released from the main anemophilous tree species growing in the Alhambra forests accounted for over 35 % of the total airborne pollen spectrum in the city of Granada. Since the remainder of the aerobiological spectrum included pollen from intensive-farmed olive groves, from the pastureland of Sierra Nevada (Poaceae), from the widely-used ornamental *Platanus hispanica* and from the ubiquitous *Parietaria* (Díaz de la Guardia et al. 2003), it may be concluded that the Alhambra forests contain sufficient numbers of trees to constitute the city's main forest mass, with all the attendant implications for the provision of associated ecosystem services (Escobedo et al. 2011). Attention is also drawn to the significant trend towards a rising PI over the study period, with an annual increase of over 1000 pollen grains. Similarly, a gradual increase in annual pollen counts was detected for most of the taxa studied; the trend was significant in the case of *Cupressus*, and only negative for *Ulmus* (Table 1). This increase may be linked to the implementation of the Alhambra Woodland Restoration Programme (2007–2015) by the Alhambra Management Board; this programme includes the diversification of tree species, involving the annual introduction of 200 specimens of *Acer*, *Quercus* and *Celtis*, as well as other species. The cypress is widely regarded as a symbol of the city; this has led to a considerable increase in the number of cypresses at historic sites (Casares-Porcel 2010). Pollen emissions by some of the tree-species present in the forests also have a marked impact on the incidence of allergies in the local population; if this trend persists in future, it is therefore likely to be accompanied by increased airborne allergen loads, leading to a deterioration in biological air quality and human health, especially given that the Alhambra forest is among the main sources of allergen emission in the city (Cariñanos et al., 2015).

The Woodland Restoration Programme also involves the replacement of trees affected by pests and diseases, and over recent years almost 2000 elms affected by Dutch Elm Disease have been replaced (Villafranca Jiménez and Salmerón Escobar 2010). This progressive removal of sick trees undoubtedly contributes to the falling trend recorded for the *Ulmus* PI, which dropped sharply after 2000. However, the replacement of *Ulmus* by *Celtis* has as yet had no impact on the pollen spectrum, since despite the large number of specimens introduced (Online Resource 1), these have not yet attained their optimum reproductive age, estimated at around 20–25 years (Verdú 2002). Moreover, this taxon has very large pollen grains and

**Table 2** Spearman's correlations between monthly meteorological parameters before and during flowering and aerobiological variables for the main tree taxa studied. *IP* Pollen Index; *SD* Start Date; *LS* Length of Season; *Rf*/ Total rainfall; *Tm* minimum Temperature; *TM* Maximum Temperature

	October			November			December			January			February			March			April			
	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	
	<i>Acer</i>	PI	-.379	-.154	.042	.355	.128	-.379	.223	-.087	.036	.298	.321	-.269	.422	.382	-.180	.007	.266	-.057	-.298	-.065
		.082	.494	.853	.105	.570	.082	.318	.701	.873	.178	.146	.226	.050	.079	.422	.976	.231	.802	.179	.773	.707
	SD	.140	-.296	-.207	-.129	.062	.012	-.169	-.119	-.168	-.022	-.350	-.379	.150	-.311	-.759**	.276	-.001	-.309	-.334	-.167	.102
		.534	.180	.355	.568	.786	.958	.453	.598	.454	.922	.110	.082	.506	.160	.000	.214	.995	.162	.129	.458	.653
	LS	-.377	-.049	.297	.124	.318	.273	-.167	-.046	.414	.244	.401	.046	.237	.553**	.002	-.219	.127	-.044	-.193	.188	.150
		.083	.827	.180	.583	.150	.219	.457	.839	.057	.274	.064	.837	.289	.008	.994	.328	.572	.844	.390	.402	.506
	PI	.596*	.243	-.382	.034	-.197	-.271	-.221	-.210	-.480*	-.351	-.238	.149	.011	.013	.450*	-.143	-.404	.079	.582**	-.390	-.490*
		.003	.276	.079	.881	.381	.223	.322	.349	.024	.110	.285	.509	.960	.954	.035	.526	.062	.726	.004	.072	.021
	SD	.163	-.036	.106	.105	.172	.104	.088	.207	.122	.197	-.145	-.210	-.029	-.125	-.538**	-.017	-.108	-.176	-.290	.146	.024
		.469	.805	.638	.643	.445	.646	.696	.355	.589	.380	.520	.349	.897	.579	.010	.940	.935	.433	.190	.516	.917
	LS	-.039	-.234	-.111	-.060	.083	-.089	-.053	-.027	-.105	-.142	-.186	.046	-.046	-.176	-.284	.154	.031	-.230	-.062	-.043	.256
		.836	.295	.622	.791	.714	.695	.814	.906	.642	.530	.407	.840	.839	.433	.201	.494	.822	.304	.783	.849	.247
	PI	-.168	-.409	.012	.030	-.350	-.051	-.142	-.313	.017	.168	-.199	-.105	.161	.107	-.106	.076	.082	.183	-.347	-.279	.027
		.456	.059	.957	.895	.110	.823	.528	.157	.941	.456	.373	.641	.473	.635	.639	.735	.716	.415	.114	.209	.904
	SD	.010	-.322	-.390	-.022	-.473*	-.418	.146	-.170	.064	.084	-.237	-.190	.366	-.228	-.368	.218	.235	-.185	-.079	-.039	-.240
		.966	.143	.073	.922	.026	.053	.516	.448	.777	.711	.288	.396	.094	.504	.308	.329	.293	.409	.728	.862	.282
	LS	.086	.199	.099	.037	.206	.202	-.023	.073	.184	-.149	.251	.373	-.309	.061	.159	.281	.251	-.059	.315	.243	-.349
		.704	.370	.073	.869	.357	.368	.918	.747	.413	.507	.260	.087	.162	.787	.481	.204	.260	.796	.154	.276	.111
	PI	-.279	.210	.427*	.265	.200	.071	.284	.217	-.068	-.102	.190	.421	.026	.367	.280	-.342	-.184	.005	.029	.182	.005
		.209	.349	.047	.232	.372	.753	.201	.331	.764	.651	.397	.051	.909	.093	.207	.120	.411	.984	.899	.412	.982
	SD	.315	-.021	-.246	.196	.065	-.116	-.117	-.077	-.118	.055	-.274	-.159	-.027	-.327	-.587**	.232	.037	-.237	-.229	.313	.207
		.153	.925	.270	.382	.773	.606	.605	.732	.601	.707	.217	.480	.903	.138	.004	.300	.871	.289	.304	.156	.355
	LS	-.390	-.046	.322	-.154	-.364	.007	.193	-.142	-.013	.198	.536*	.175	.269	.609**	.187	.086	.298	-.373	.133	.222	-.038
		.072	.838	.131	.493	.096	.976	.389	.528	.954	.378	.010	.437	.226	.003	.406	.704	.178	.088	.556	.321	.866

Table 2 (continued)

	October			November			December			January			February			March			April			
	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	Rf	Tm	TM	
<i>Quercus</i>	PI	-.342	-.102	.036	-.009	-.246	-.164	.129	-.322	-.331	-.054	.064	.087	.179	.271	.029	-.172	-.107	-.033	-.139	-.408	-.261
		.119	.651	.873	.968	.269	.465	.568	.144	.132	.813	.776	.700	.425	.223	.897	.443	.634	.885	.536	.059	.241
	SD	.197	-.156	-.232	.053	.021	-.060	-.154	-.162	-.166	.090	<b>-.432*</b>	-.365	.102	-.397	<b>-.750**</b>	.217	-.200	-.364	-.112	.050	.003
		.380	.489	.299	.814	.924	.792	.493	.490	.459	.691	<b>.045</b>	.095	.652	.068	<b>.000</b>	.332	.372	.096	.620	.824	.989
	LS	-.037	-.109	-.046	-.270	-.394	.010	.214	-.036	.194	-.292	-.089	.328	.059	.172	.287	.002	.038	-.006	.135	-.321	-.411
		.871	.631	.838	.224	.070	.965	.338	.875	.387	.187	.693	.136	.793	.445	.195	.992	.866	.979	.551	.145	.058
<i>Cupressus</i>	PI	-.173	.119	.110	<b>.490*</b>	-.003	-.312	.262	-.055	-.200	.239	.258	-.006	.199	.389	-.002	-.098	-.530	-.303	.328	.117	-.357
		.440	.597	.627	<b>.021</b>	.990	.158	.240	.806	.373	.284	.247	.980	.375	.074	.994	.665	.496	.170	.136	.604	.103
	SD	-.380	.180	.278	<b>.596**</b>	.292	-.228	<b>.459*</b>	.383	-.250	<b>.496*</b>	<b>.449*</b>	.005	.036	.290	.132	.086	.257	.051	-.176	.414	<b>.426*</b>
		.081	.422	.210	<b>.003</b>	.187	.309	<b>.032</b>	.079	.262	<b>.019</b>	<b>.036</b>	.983	.875	.190	.557	.704	.249	.822	.434	.055	<b>.048</b>
	LS	.175	.177	-.103	-.125	<b>-.442*</b>	-.334	.120	-.186	-.269	.247	-.107	-.098	-.172	.004	-.410	-.024	-.188	-.391	-.203	.187	.078
		.437	.431	.647	.578	<b>.039</b>	.128	.596	.407	.227	.268	.636	.666	.445	.986	.058	.915	.403	.071	.365	.405	.731

\*significant value at  $p < 0.05$

\*\*significant value at  $p < 0.1$

**Table 3** Stepwise multiple regression model of monthly meteorological parameters on annual Pollen Index for the various taxa

TAXA	Model	R <sup>2</sup> corr.	
<i>Acer</i>	1	0.23	IP = 4135.28–191.76NTM + 589.91
	2	0.53	IP = 6245.04–279.27NTM–17.32ApRf + 472.19
	3	0.65	IP = 6034.2–276.53NTM–7.66ApRf + 119.11FTmin + 415.21
	4	0.72	IP = 8262.6–277.67NTM–21.35ApRf + 120.29FTmin–98.06ApTM + 379.38
<i>Ulmus</i>	1	0.37	IP = 141.29 + 3.15ORf + 140.97
	2	0.52	IP = 173.39 + 4.20ORf–2.11MRf + 125.7
	3	0.62	IP = 121.05 + 3.35ORf–2.21MRf + 2.81ApRf + 114.52
<i>Corylus</i>	1	0.51	IP = –5.931 + 0.567NRf + 26.58
	2	0.61	IP = 3.294 + 0.613NRf–0.268JRF + 24.48
	3	0.71	IP = –7.695 + 0.612NRf–0.338JRF + 0.379FRf + 21.77
<i>Pinus</i>	1	0.21	IP = –1259.19 + 159.52JTM + 455.96
	2	0.38	IP = –1917.57 + 191.86JTM + 3.85DRf + 413.07
<i>Quercus</i>	1	0.23	IP = 8710.35–781.74ApTmin + 1658.76
	2	0.40	IP = 10,095.11–830.64ApTmin–22.76ORf + 1503.34
	3	0.66	IP = 24,815.3–681.84ApTmin–29.35ORf–1106.67DTM + 1169.79
<i>Cupress.</i>			No variable was included in the model

IP Pollen Index; NTM November Maximum Temperature; ApRf April Total Rainfall; FTmin February minimum Temperature; ApTM April Maximum Temperature; ORf/October Total Rainfall; MRf/March Total Rainfall; JTM January Maximum Temperature; DRf/December Total Rainfall; ApTmin April minimum Temperature; DTM December Maximum Temperature

therefore a low dispersal rate (Nitiu 2003), and hence does not even account for 1 % the total airborne pollen spectrum.

Spearman's correlation analysis for monthly weather patterns and airborne pollen parameters revealed that, for spring-flowering perennials (*Pinus* and *Quercus*), the most influential factors were temperature and rainfall over the months immediately prior to flowering, i.e. during the previous autumn and winter; while for winter-flowering deciduous species (*Acer*, *Ulmus*, *Corylus*), the influence of these factors persisted even during the flowering period, as part of an overall process known as “readiness to flower” (Linskens and Cresti 2000).

This was confirmed by the PI prediction models obtained by stepwise multiple regression: while models for *Pinus* and *Quercus* included rainfall over several months before flowering, resulting in a long-term period of accumulation of water (Pinto et al. 2011), *Ulmus* and *Acer* models included April rainfall (i.e. after flowering), highlighting the need for these species to keep accumulating water during the vegetative period as part of their ongoing adaptation to water stress (Gálmez et al. 2007; Romanovskaja et al. 2012). Most significant was the case of *Corylus*, in which the only variables included in the models were rainfall in November, January and February, in contrast to findings for other areas in which temperature over the months prior to flowering has proved to be the most significant variable (Crepinsek et al. 2012).

Analysis of correlations between weather patterns over the months prior to flowering and up until the peak annual pollen count (Table 2) revealed a significant correlation between winter temperatures and phenology in all species, both winter-flowering (*Acer*, *Corylus*, *Ulmus*, *Cupressus*) and spring-flowering (*Pinus*, *Quercus*). This reflects inter-species

differences in chilling and heat accumulation requirements. In order to break dormancy. For winter-flowering deciduous species, accumulation of threshold temperatures starts in December and may continue into the pollination period (Myking 1999; Crepinsek et al. 2012), whereas spring-flowering species have higher thresholds and need longer to attain them (Nienstaedt 1967; Pinto et al. 2011). For *Quercus ilex subsp. Rotundifolia*, for example, the threshold temperature has been set at 7 °C, so the time required to attain that temperature includes the winter and spring months (Jato et al. 2007).

*Cupressus* was considered separately in this analysis, since—although it is the taxon showing the strongest correlation with weather-related parameters—no variable was included in the formula using weather data as independent variables (Table 3). Interestingly, *Cupressus* recorded the most marked increase in PI throughout the series, by almost 1000 pollen grains per year, together with a lengthening of the flowering period by more than 2 days per year. This may be due to the increase in the number of *Cupressus* trees in the city (Cariñanos et al., 2015), and to the large number of species growing locally, but may also be related to the drop in minimum winter temperatures recorded in the study area over the last 30 years (Cariñanos et al., 2013); several authors have drawn attention to the influence of this latter parameter on the PI (Galán et al. 1998). Nevertheless, the specific phenological and reproductive behaviour of the various species present in the area makes it difficult to establish a general prediction model. *Cupressus* pollen is currently a key allergen in the local population, with a reported incidence of over 30 %. If this rising trend continues, *Cupressus* pollen would clearly be one of the major allergens in future climate-change scenarios (Beggs 2004).

However, these results have to be examined within the context of current climate evidence and future scenarios, especially since the impact of climate change on pollen production may be indicative of alterations in forest productivity. With regard to current climate evidence, while trends in seasonal maximum and minimum temperatures and in seasonal rainfall over the study period were in line with general data for the Iberian Peninsula, with a both significant increase in temperature and a decline in rainfall mostly in summer (EEA 2012; Haylock et al. 2008), this study found no significant negative effect on pollen counts for the species considered, due in part to management of this type of forest, with an annual increase in the number of trees and additional water intake during the summer.

The climate conditions expected over the coming years in the Mediterranean region may have a major impact on future pollen emissions. According to the latest IPCC report, by the end of the century, the average winter temperatures may be up to 3.8 °C higher than today (Kovats et al. 2014). This would mainly affect plant reproductive stages, prompting an advance in flowering which would be more pronounced in spring-flowering species (Wolkovich et al. 2012; Peñuelas et al. 2002), and more marked in anemophilous than in entomophilous species (Gordo and Sanz 2005). The IPCC report also forecasts a drop in precipitation, by up to 24 % for summer rainfall and 12 % for winter rainfall. Given this scenario, there is likely to be a reduction in the intensity of pollen emissions, at least from species with strict environmental requirements during the growing period, such as *Acer*, *Ulmus* and *Corylus* (Awada and Josiah 2007).

These restrictive conditions may even affect Mediterranean evergreen species (*Pinus*, *Quercus* and *Cupressus*), which have a marked ability to tolerate disturbances and drought periods over short periods (Lloret et al. 2004; Calamassi et al. 2001). Another potential consequence could be a decline in net carbon absorption by forest ecosystems under extreme climate conditions, i.e. very hot, dry years, when net absorption may be 20 to 30 % lower than in normal conditions (Scarascia-Mugnozza et al., 2000). Even species well adapted to

Mediterranean climate conditions (e.g. *Quercus ilex*) display decreasing net CO<sub>2</sub> uptake values at high temperatures (Ogaya and Peñuelas 2003). Finally, a change in the seasonal rainfall regime may also substantially alter net ecosystem productivity (NEP) due to the detrimental effect of water stress on gross primary production (Allard et al. 2008). This combination of factors could in turn have an effect on pollen production, because while species with greater adaptive capacity would be at greater advantage in water-stress conditions, and some may even produce more pollen when CO<sub>2</sub> concentrations are high (Rogers et al. 2006), in other species drought may give rise to a greater economy of pollen production (Saini 1997). Moreover, plants may be more vulnerable to pests and diseases (Allard et al. 2008), and in the case of the forests of La Alhambra, limited water availability may have accelerated the response of *Ulmus* to Dutch Elm Disease (Solla and Gil 2002).

Given that not all Mediterranean species will show the same physiological response to environmental changes (Ogaya and Peñuelas 2003), the projected climate scenarios might be expected to prompt a reduction in total pollen emissions by species growing in the Alhambra forest; the decline could be especially marked in the case of deciduous species. However, is it also possible that interspecific interactions taking place in mixed-species forests could enhance and increase nitrogen and light absorption (Forrester 2014), as well as enhancing resilience under new climate conditions (Archaux and Wolters, 2006). This highlights the importance of management strategies aimed at mitigating the impact of climate change and maintaining the positive ecosystem services; such measures—including the strengthening of individuals, diversification, and the replacement of individuals affected by pests—are implemented on a regular basis in this semi-natural forest.

In conclusion, analysis of pollen-count trends over time for the main wind-pollinated species in the Alhambra forest suggests that pollen-release is an extremely valuable indicator of the response of different species to changing climate conditions, of their capacity to recover after disturbance, and of the overall response of the forest mass to future potential disturbances.

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