

Long-range transport of beech (*Fagus sylvatica* L.) pollen to Catalonia (north-eastern Spain)

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Abstract Local and long-range transport of beech (*Fagus sylvatica*) pollen was analysed by using 23-year data (1983–2007) at six stations in Catalonia, Spain, and numerical simulations. Back trajectories and synoptic meteorology indicated a consistent north European provenance during beech pollen peak days. Specifically, the area from northern Italy to central Germany was the most probable source, as indicated by a source-receptor model based on back trajectories. For the event with the highest pollen levels (17 May 2004), back trajectories indicated a source in the Vosges (NE France) and the Schwarzwald (SW Germany) regions. By applying a mesoscale model (MM5) to this event, pollen transport could be further refined, allowing its entrance to Catalonia through the lower easternmost pass of the Pyrenees (the Alberes pass, 500 m a.s.l.) to be described. Hourly counts of *Fagus* pollen allowed the timing of pollen arrival during this

episode to be matched with the model results regarding the above-mentioned passage. This study may help to interpret some results of modern beech genetic diversity and contribute to the understanding of paleopalynological records by taking long-range transport into consideration.

Keywords Pollen · Back trajectories · Source receptor model · Mesoscale transport model

Introduction

Small-sized biological material, such as microorganisms, fungal spores, plant diaspores (pollen) and small seeds can be suspended in the atmosphere and transported with the wind. In some circumstances, large pulses are injected into the atmosphere, from where they can be dispersed for hundreds of kilometres (Kellogg and Griffin 2006). There is increasing interest in the entrainment and transport of such biological material to distant places because of its important consequences for (1) the transport of pathogens, (2) the expansion of the biogeographical ranges of different organisms, and (3) health effects due to the dispersion of allergenic pollen.

For most plant species, pollen plays an important role in shaping the genetic structure of populations (Burczyk et al. 2004), being responsible for gene flow (Ellstrand 1992; Ennos 1994), and contributing to the spatial distribution of the species (Ellstrand 1992; Schmidt-Lebuhn et al. 2007; Sharma and Kanduri 2007; Smouse et al. 2001). The study of gene dispersal by pollen has important implications for plant biogeography and plant conservation biology. Therefore, a proper understanding of pollen dispersal is important for the management and conservation of plant species in increasingly fragmented landscapes. Specifically, pollen

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dispersal is a crucial process in the life cycle of wind-pollinated plants.

Many palynological studies have analysed airborne pollen dispersion. The extent of this transport can vary from a few metres to thousands of kilometres. To frame the dispersion scale, Prentice (1985) proposed a spatial classification from a local range comprising an area of 20 m radius, to an extra-regional scale for distances greater than 200 km. The long-range transport of pollen and spores invoking the extra-regional scales has recently attracted much attention. For example, it has been demonstrated that viable microorganisms and fungal spores sampled in Barbados (Southern Caribbean Sea) were transported westwards with dust plumes from Africa, thus travelling more than 4,000 km (Prospero et al. 2005). Moreover, African mineral dust together with biological material has been sampled in France (van Campo and Quet 1982) and as far north as Scandinavia (Franzen et al. 1994). Other long-range transports, from south to north, are evidenced by the recording of “exotic” pollen grains in Fennoscandia originating in the Mediterranean (van Hjelmsroos 1991), and the finding in the Arctic environment of pollen from trees forming forests at much lower latitudes (Bourgeois 2000; Hicks and Isaksson 2006; Rousseau et al. 2003, 2006). Also, particles from long-range transport have been found in the Antarctic (Wynn-Williams 1991) and Australia (Hart et al. 2007).

Some recent studies have described the long-range transport of allergenic pollen (Cecchi et al. 2006; Hjelmsroos 1992; Stach et al. 2007). Under some circumstances this long-range transport may cause pre-seasonal pollen episodes, which are currently not included in forecasts based only on local phenological observations, since the pollen may arrive from localities with more advanced flowering seasons (Skjoth et al. 2007). For high allergenic pollen, this poses a difficulty for the protection of allergic patients, and requires that atmospheric transport models that account for long-range transport are included in forecasting schemes.

In Europe, the determination of the origin of airborne *Fagus* pollen is fundamental to the documentation of the range of dispersal of beech pollen. *Fagus* pollen can be responsible for allergic manifestations when abundant (Frei and Leuchner 2000; Heinzerling et al. 2005; Ickovic and Thibaudon 1991; Lewis et al. 1983). Therefore, an understanding of pollen dispersal is urgently required by the European health care system.

In this work, we have concentrated on the pollen dispersal of beech (*Fagus sylvatica* L.) over Catalonia. Beech trees are widely distributed across Europe except for most of Spain. The aim of this work was to analyse the role of long-distance transport in determining the concentration of airborne *Fagus* pollen observed in the pollen records from six stations across Catalonia (Fig. 1). A case for long-

range pollen transport in the Catalan area was already documented for *Ambrosia coronopifolia*, when unusual atmospheric circulation conditions brought air masses from the area of Lyon (France), where this species is abundant, to Catalonia (Belmonte et al. 2000).

To discriminate between the long-range transport of *Fagus* pollen and the influence of local pollen, we hypothesised that long-distance transport would be indicated by simultaneous peaks at the majority of the Catalan monitoring stations, taking into account that *Fagus* plants are not present around most of them. Subsequently, we used back trajectories and mesoscale wind movements to describe the synoptic flux responsible for the transport for the days of pollen arrival. Finally, we applied a source–receptor model to infer the probable source regions of the *Fagus* pollen arriving in Catalonia.

Our study may contribute to the interpretation of some results pertaining to modern genetic diversity, and help palaeopalynologists in understanding their pollen records by taking long-range transport in consideration.

Materials and methods

Fagus sylvatica L. (European beech) is a large deciduous tree of the Fagaceae family. It is present throughout most of central Europe, including the northern Spanish border, southern Britain, Italy, the Balkans, southern Scandinavia and Eastern Europe (Fig. 1). European beech is usually found on chalky soils and limestones but is tolerant of a wide range of soils and conditions (Rocha Afonso 1990). In its northern ranges, European beech represents the dominant species of the lowlands (Puhe and Ulrich 2001); however, in southern and south-central Europe, beech occurs mainly at higher elevations and is often associated with silver fir (*Abies alba*). In Spain, it forms dense forests in mountain slopes between 500 and 2,000 m under fresh and humid climates with an average rainfall of over 1,000 mm year⁻¹ (Rocha Afonso 1990). Where summers are dry, it needs high atmospheric humidity, and late spring frosts are lethal to flowers (Terradas 1984). In Spain, conditions of humidity and temperature adequate for beech development are found only in the northern mountain ranges (the Pyrenees, Cantabric range) and in some isolated locations (north of the Sistema Ibérico, Sistema Central and Puerto de Beceite; Rocha Afonso 1990).

Beech is a shade-tolerant tree that attains flowering maturity after approximately 40 years of age. Pollination is anemophilous. Male flowers (producing the pollen) are spheroid catkins that appear simultaneously with leaves. In Spain this happens from March to May (Bolòs and Vigo 2005) or from April to June (Rocha Afonso 1990). Flowering and fruiting usually occurs in alternate years

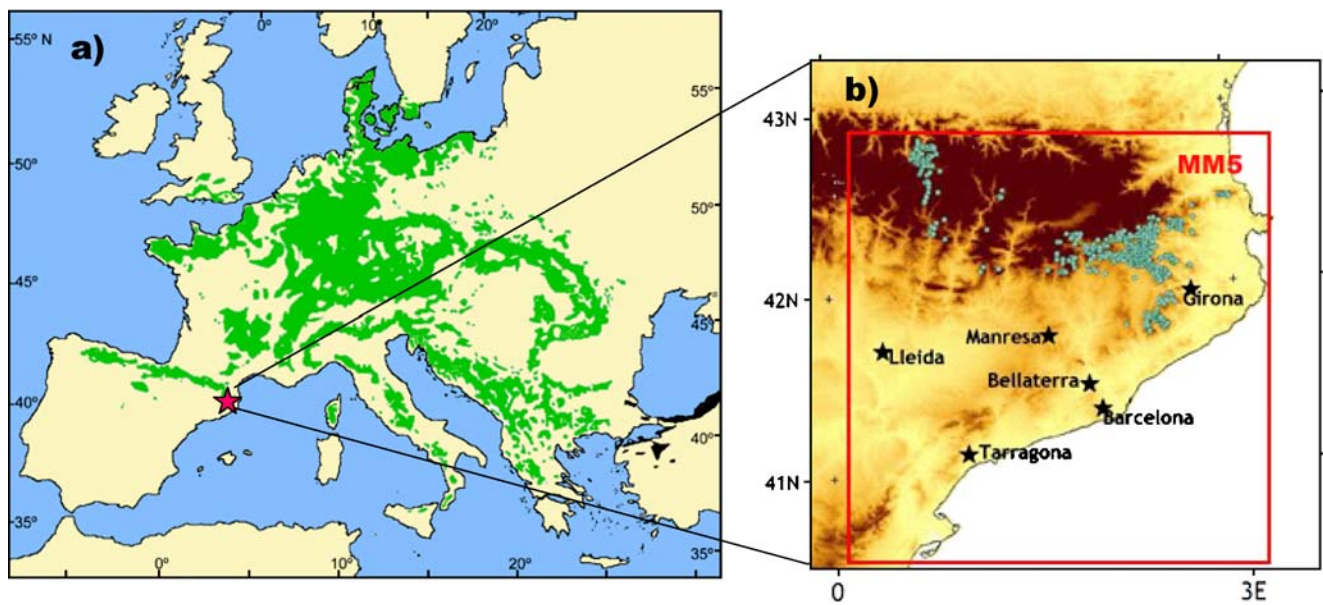


Fig. 1 **a** *Fagus* distribution map in Europe, from Magri et al. (2006). **b** Catalonia, showing the mesoscale model (MM5)-model domain, sampling sites and inventory plots with *Fagus* (blue circles). Catalan beech distribution was compiled from inventories

available from IEFEC (Inventari Ecològic i Forestal de Catalunya, <http://www.crea.uab.es/ieffc/>) and IFN2 (Inventario Forestal Nacional, <http://www.mma.es/portal/secciones/biodiversidad/inventarios/ifn>)

with a biannual rhythm per tree (annual in some adults) and between 4 and 7 years for the whole forest (Terradas 1984).

Pollen record

Pollen data were recorded at six monitoring stations across Catalonia, NE Spain: Barcelona, Bellaterra, Girona, Lleida, Manresa, and Tarragona (Fig. 1). Samples were obtained weekly from a Cour sampler (Cour 1974) for the period 1983–1995, and daily from a Hirst sampler (Hirst 1952)—the standardised method in European aerobiological networks, from 1996 onwards. The total recording period was 23 years, from 1983 to 2007 inclusive (except for the years 1986 and 1987). Details of the sampling schedule at the different locations are shown in Table 1. Because of the seasonal character of the pollen emission, which is linked to flowering, pollen counts used in this paper comprise the period from 1 March to 1 July each year.

Pollen peak identification

By analysing the complete temporal series of daily data, one can conclude that outstanding *Fagus* pollen concentrations were present in 2004 and 2006 (Table 2). Annual indexes recorded an absolute maximum in year 2004 at all sites and a second maximum in 2006, in four out of the six sites (Table 3). For this reason, these years were analysed in more detail: each monitoring station was screened to detect peaks of pollen arrival by using a paired t-test that compared pollen counts on consecutive days. Moreover,

the complete data set was screened to identify the dates of maximum absolute concentration (see Table 2).

Atmospheric transport

The provenance of the air-masses transporting pollen was examined using backward atmospheric trajectories. Isentropic 96-h back-trajectories at 1,500 m a.s.l., starting at 12 UTC from the coordinates of each monitoring site or from a central point in the Catalan geographical area (41.8° N, 1.5° E) were computed using the Hybrid Single-Particle Lagrangian Integrated Trajectory model (HYSPLIT-4) of the National Oceanic and Atmospheric Administration (NOAA) (available at <http://www.arl.noaa.gov/ready/hysplit4.html>, Draxler and

Table 1 Geographical and climatic characteristics of the Catalan aerobiological stations

Station	Geographical characteristics		Climatic characteristics	
	Altitude (m)	Geographical coordinates	Mean annual temperature (°C)	Annual rainfall (mm)
Barcelona	93	41°24'N, 02°09'E	16.4	593
Bellaterra	245	41°33'N, 02°06'E	15.2	594
Girona	98	41°59'N, 02°50'E	15.0	740
Lleida	202	41°37'N, 00°38'E	15.1	385
Manresa	291	41°44'N, 01°30'E	13.6	619
Tarragona	44	41°07'N, 01°15'E	15.8	478

Table 2 *Fagus* pollen absolute peaks in Catalan stations for the period 1983–2007 and the corresponding back trajectories

Year	Date	Locality	Peak concentration (pollen grains/m ³)	Back trajectory
1984	Week 19 (7–13 May) ^a	Seu d'Urgell ^a	1.4 ^a	N
1985	Week 21 (20–26 May) ^a	Barcelona ^a	1.6 ^a	Several, NE included
1989	Week 18 (1–7 May) ^a	Girona ^a Tarragona ^a	8.7 ^a 6.5 ^a	N
	Week 20 (15–21 May) ^a	Barcelona ^a Bellaterra ^a	9.1 ^a 1.0 ^a	Several, N included
1990	Week 17 (23–29 April) ^a	Barcelona ^a Bellaterra ^a Girona ^a	1.0 ^a 1.4 ^a 1.5 ^a	N
1991	Week 21 (20–26 May) ^a	Tarragona ^a	1.8 ^a	N
	Week 23 (3–9 June) ^a	Bellaterra ^a	1.2 ^a	N and NW
1992	Week 18 (27 April–3 May) ^a	Barcelona ^a Bellaterra ^a	2.5 ^a 2.4 ^a	N and NW
	Week 19 (4–10 May) ^a	Girona ^a	6.9 ^a	N and NW
	Week 20 (11–17 May) ^a	Lleida ^a	2.3 ^a	Several, N included
1994	Week 17 (16–22 April) ^a	Girona ^a	2.0 ^a	Several, N included
	27 April	Bellaterra	1.4	N
	3 May	Barcelona	1.4	W
1995	Week 15 (10–16 April) ^a	Lleida ^a Bellaterra ^a	4.4 ^a 1.8 ^a	N
	13 April	Bellaterra	4.9	NE
	Week 17 (24–30 April) ^a	Girona ^a	3.7 ^a	several
	2 May	Barcelona	4.2	N
	Week 19 (8–14 May) ^a	Tarragona ^a	1.1 ^a	NNW
	14/05	Girona	1.4	N
1996	Week 16 (14–20 April) ^a	Bellaterra ^a	1.6 ^a	Several, N included
1997	4 April	Girona	9.8	N
	16 April	Lleida	4.9	N
	21 April	Barcelona Bellaterra Tarragona	4.9 5.6 2.1	NE
1998	15 May	Girona Tarragona	21 1.4	N
1999	22 April	Bellaterra	2.8	W
	3 May	Manresa	7.0	E to N
	12 May	Lleida Girona	4.2 18.9	SW
	13 May	Barcelona	8.4	SW
	14 May	Tarragona	2.8	W
2000	7 May	Girona	2.1	E
2001	29 May	Girona	2.8	NW

Table 2 (continued)

Year	Date	Locality	Peak concentration (pollen grains/m ³)	Back trajectory
		Bellaterra	1.4	
		Barcelona	1.4	
	31 May	Lleida	1.4	N and NW
2002	21 April	Barcelona	4.2	NE
		Bellaterra	3.5	
	25 April	Girona	18.9	N
	26 April	Lleida	2.8	NW
2003	13 May	Girona	1.4	W
2004	17 May	Lleida	91.0	NE
		Bellaterra	38.5	
		Girona	37.8	
		Barcelona	37.1	
		Manresa	29.4	
		Tarragona	26.6	
2005	19 April	Manresa	2.8	W
	9 June	Tarragona	1.4	N
2006	25 April	Manresa	9.1	N (local)
	26 April	Barcelona	7.0	NW
		Bellaterra	2.8	
	29 April	Girona	32.9	NW
		Tarragona	12.6	
		Lleida	6.3	
2007	23 April	Lleida	2.8	E
	4 May	Bellaterra	3.5	NW
		Girona	5.6	NW

^a Cour data

Rolph 2003) from the gridded meteorological fields of the FNL archive data. According to the area crossed by the backward trajectories, the trajectory origin was classified as coming from Africa (AF), the Mediterranean (ME), the Iberian Peninsula (PE), Europe (EU) or the Atlantic Ocean (AT).

The Fifth-Generation Pennsylvania State University/ National Center for Atmospheric Research (PSU/NCAR) Mesoscale Model (MM5) (<http://www.mmm.ucar.edu/mm5/mm5-home.html>) was used to simulate some specific meteorological situations corresponding to days with exceptionally high pollen levels. MM5 is a limited-area, non-hydrostatic, terrain-following sigma-coordinate model designed to simulate or predict mesoscale atmospheric circulation (Dudhia 1993; Grell et al. 1994). Initialisation and boundary conditions were updated every 6 h from the analysis data of the European Centre for Medium Range Weather Forecast (ECMWF). Meteorological simulations were performed using three nested domains with 9, 3 and

Table 3 Annual pollen indexes (API = sum of daily counts) registered for *Fagus* pollen in Catalonia for the period 1983–2007

Year	Barcelona	Bellaterra	Girona	Lleida	Manresa	Tarragona
1983	10.3 ^a					
1984	1.6 ^a					
1985	27.5 ^a					
1988	1.3 ^a	2.8 ^a				
1989	78.1 ^a	14.1 ^a	108.9 ^a			65.8 ^a
1990	9.2 ^a	18.0 ^a	22.3 ^a			4.0 ^a
1991	8.6 ^a	22.0 ^a	12.2 ^a			14.7 ^a
1992	43.7 ^a	45.3 ^a	101.0 ^a	49.8 ^a		6.6 ^a
1993	2.6 ^a	0.0 ^a	2.4 ^a	4.3 ^a		0.6 ^a
1994	2.8 ^b	7.7 ^b	40.1 ^a	10.0 ^a		0.5 ^a
1995	16.1 ^b	25.9 ^b	41.2 ^a	58.7 ^a		14.8 ^a
1996	1.4 ^b	0.7 ^b	3.5 ^b	0.0 ^b	0.0 ^b	0.0 ^b
1997	21.7 ^b	20.3 ^b	63.7 ^b	18.2 ^b	7.7 ^b	7.0 ^b
1998	1.4 ^b	5.6 ^b	9.1 ^b	2.1 ^b	0.0 ^b	1.4 ^b
1999	16.1 ^b	18.2 ^b	130.2 ^b	16.1 ^b	21 ^b	10.5 ^b
2000	1.4 ^b	1.4 ^b	4.2 ^b	0.0 ^b	0.0 ^b	0.0 ^b
2001	2.1 ^b	2.8 ^b	7.0 ^b	2.1 ^b	0.0 ^b	0.7 ^b
2002	21.0 ^b	21.0 ^b	142.8 ^b	11.2 ^b	16.1 ^b	2.8 ^b
2003	1.4 ^b	0.7 ^b	5.6 ^b	0.0 ^b	0.0 ^b	1.4 ^b
2004	127.4 ^c	126.7 ^c	338.1 ^c	169.4 ^c	130.9 ^c	92.4 ^c
2005	2.8 ^b	2.8 ^b	16.8 ^b	0.7 ^b	2.8 ^b	4.9 ^b
2006	19.6 ^c	18.2 ^b	109.2 ^b	28.0 ^b	55.3 ^b	39.2 ^b
2007	2.8 ^b	9.8 ^b	31.5 ^b	1.4 ^b	8.4 ^b	28.0 ^b
Absolute max	127.4 ^c	126.7 ^c	338.1 ^c	169.4 ^c	130.9 ^c	92.4 ^c
Year	2004 ^c	2004 ^c	2004 ^c	2004 ^c	2004 ^c	2004 ^c
Second max	19.6 ^c	25.9 ^c	142.8 ^c	28.0 ^c	55.3 ^c	39.2 ^c
Year	2006 ^c	1995 ^c	2002 ^c	2006 ^c	2006 ^c	2006 ^c

^a Cour data^b Hirst data^c Absolute API maximum data

1 km horizontal resolutions. For these specific situations, back trajectories were computed from the velocity fields obtained from the MM5 inner domain simulations (1 × 1 km² resolution, Fig. 1) using a purely kinematic trajectory model (Alarcón et al. 1995).

Source areas

A statistical approach that combines pollen concentration data at the receptor stations with backward trajectories ending at these sites was applied to infer the source areas of the pollen reaching the Catalan stations. Such source–receptor methodologies establish a relationship between a receptor point and the probable source areas by associating each value of pollen abundance with its corresponding back-trajectory. A grid with 2,601 cells of 1° × 1° latitude and longitude was then superimposed on the integration region of the trajectories in order to map the contributing points.

We applied Seibert methodology (Seibert et al. 1994), in which a logarithmic mean pollen concentration is computed for each grid cell based on the residence time of the trajectories in the cells:

$$\log C_{ij} = \frac{\sum_l n_{ijl} \log C_l}{\sum_l n_{ijl}}$$

where C_{ij} is the mean concentration in the (i,j) cell, l is the index of the trajectory, n_{ijl} is the number of time steps of the trajectory l in the cell (i,j), and C_l is the pollen concentration measured at the receptor point corresponding to the trajectory l . For this calculation, daily back trajectories from 1 April to 30 June for the 10-year period 1997–2006 (720 trajectories) were used. Segment end points corresponded to 60-min time steps (69,120 end points). The accuracy of the methodology increases with the number of end points considered; therefore, we used the maximum meteorological data available for the calculations (period 1997–2006). To minimise the uncertainty of the trajectories, a smoothing method was applied and the value of each cell was replaced by the average of that cell and the eight neighbouring cells. Finally, a filter was applied to exclude cells with less than five time-steps. The abundance field map obtained in this way reflects the contribution of each cell to the abundance at the receptor point.

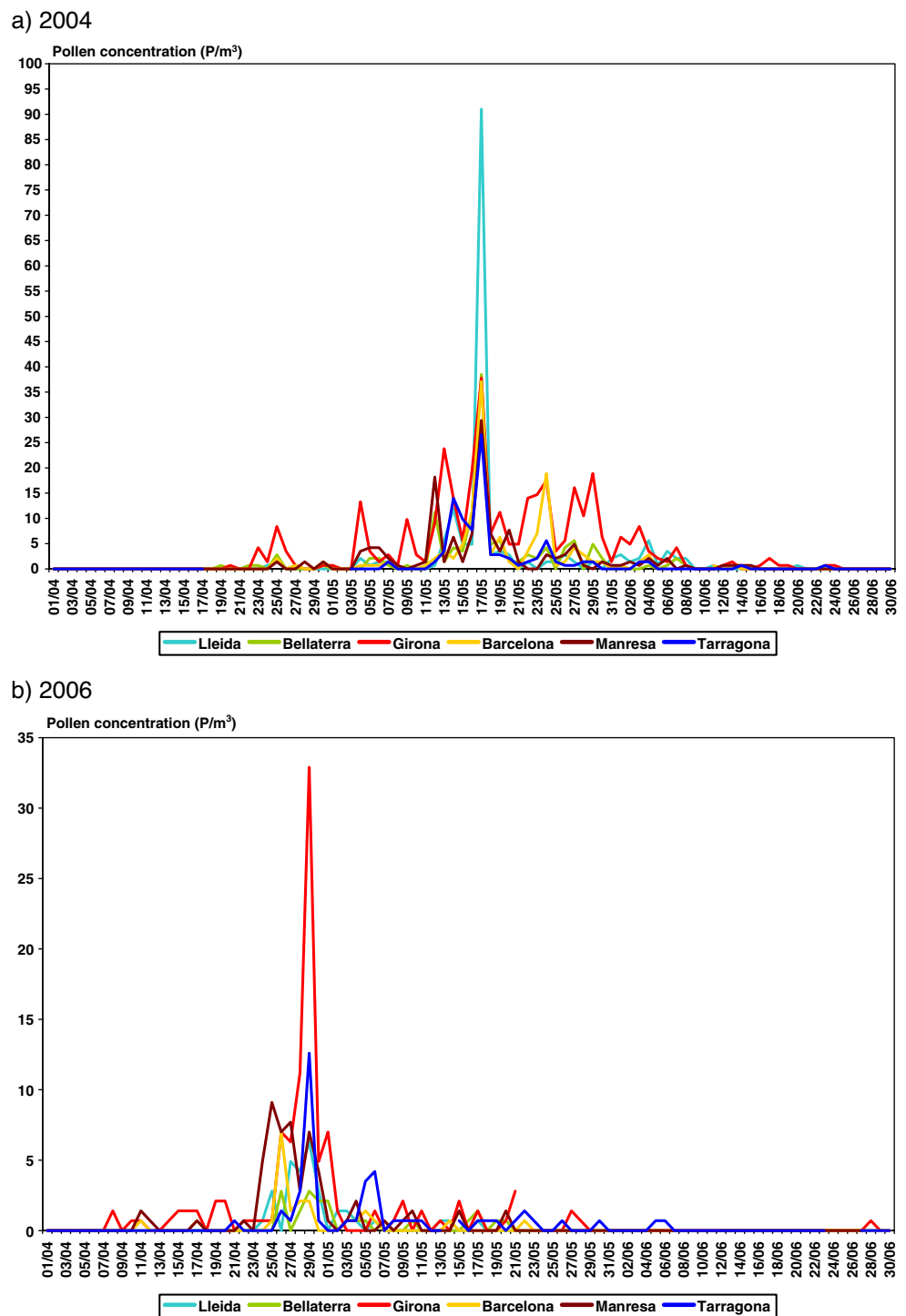
Results and discussion

Peak dates and wind trajectories

The data revealed that the dates of yearly absolute maximum concentrations at the Catalan stations for the whole study period have predominantly North wind trajectories (Table 2). By considering only data obtained with Hirst samplers (daily basis), years 2004 and 2006 presented the highest *Fagus* pollen concentrations in the whole 14-year recording period (Tables 2, 3). Therefore, these two years were selected for more detailed study. The temporal variation in the mean daily pollen concentrations in 2004 and 2006 for the six recording stations is shown in Fig. 2. During 2004, the highest mean daily pollen concentrations at all Catalan stations were recorded on 16–17 May. In 2006, most of the stations recorded the largest concentrations during the period 26–29 April.

Synoptic flux and back trajectories were used to infer the origin of the air masses reaching the stations during these particular days (Table 4). During 2004, all peak days, except for 9 and 30 May, presented air fluxes

Fig. 2 Mean daily airborne *Fagus* pollen concentrations in the Catalan stations from 20 April to 30 May in **a** 2004 and **b** 2006



originating in northern Europe. For wide coverage events (i.e. when peaks were detected simultaneously in three or more of the Catalan stations, as was the case on the 25 April, and 12, 13, 14, 16 17, 22, 24 and 27 May 2004), all the back trajectories originated in northern Europe (Table 4). In contrast, during 2006, the pollen peaks were associated with more diverse provenances: northern

European air mass fluxes (31%) and Mediterranean (34%) presented similar frequencies, while Atlantic and Peninsular back trajectories accounted only for 17% and 14%, respectively, of the peak days. Nonetheless, for broad scale events covering three or more stations, the dominant quadrant was again northern Europe (75% of cases; see Table 4).

Table 4 Dates for *Fagus* pollen peaks in 2004 and 2006. The stations where the peak was observed and the provenance of the air mass according to Hysplit back trajectories are also shown. Sampling stations: *B* Barcelona, *Be* Bellaterra, *G* Girona, *LL*leida, *M* Manresa, *T*Tarragona. Provenances: *AF*African, *AT*Atlantic, *EU*European, *ME*Mediterranean, *PE*Iberian Peninsular

2004			2006		
Date	Sampling stations	Trajectory origin	Date	Sampling stations	Trajectory origin
23 April	G	EU	21 April	T	AT
25 April	BBeGM	EU	22 April	M	AF
30 April	M	EU	24 April	LM	ME
4 May	GM	EU	25 April	BLM	ME
5 May	Be	AT or EU	26 April	BBeGT	EU
6 May	Be	EU	27 April	LM	EU
7 May	T	EU	28 April	BBeGT	EU
9 May	G	AT	29 April	GLMT	EU
12 May	BeGMT	EU	1 May	G	EU
13 May	GLT	EU	2 May	L	ME
14 May	LMT	EU	3 May	BeMT	ME
15 May	B	EU	4 May	M	ME
16 May	BBeGM	EU	5 May	BT	ME
17 May	BBeGLMT	EU	6 May	GL	EU
19 May	B	EU	7 May	BeM	ME
20 May	M	EU	8 May	T	AT
22 May	BBeG	PE or EU	9 May	GM	AT
24 May	BGMT	EU	10 May	BeM	PE
26 May	BeG	EU	11 May	G	PE
27 May	BBeGM	EU	13 May	L	ME
29 May	BeG	EU	14 May	B	ME
30 May	M	PE	15 May	GMT	ME
31 May	G	EU	16 May	Be	ME
1 June	G	EU	17 May	BBeGT	PE
3 June	T	EU	19 May	Be	AT
4 June	BM	EU	20 May	M	AT
6 June	M	EU	21 May	GT	PE
7 June	BeG	EU	22 May	BT	PE
			26 May	T	EU
			27 May	G	EU
			30 May	T	EU
			6 June	T	EU

To study the influence of local vegetation on the pollen records, Girona and Barcelona stations were examined in more detail. Contingency table tests indicated a significant association between pollen peaks and European provenance at Girona for both 2004 and 2006 (Table 5). At the Barcelona station, this association was significant only in 2004, where 100% of the peak events corresponded to European air masses. In 2006, only six pollen peak events were recorded in Barcelona, 50% of which had a European origin (Table 5).

The above lines of evidence suggest that peak days of *Fagus* pollen in the Catalan stations are associated with northern European air masses. However, to better describe

the transport, an outstanding pollen event on 16–17 May 2004 was studied in more detail.

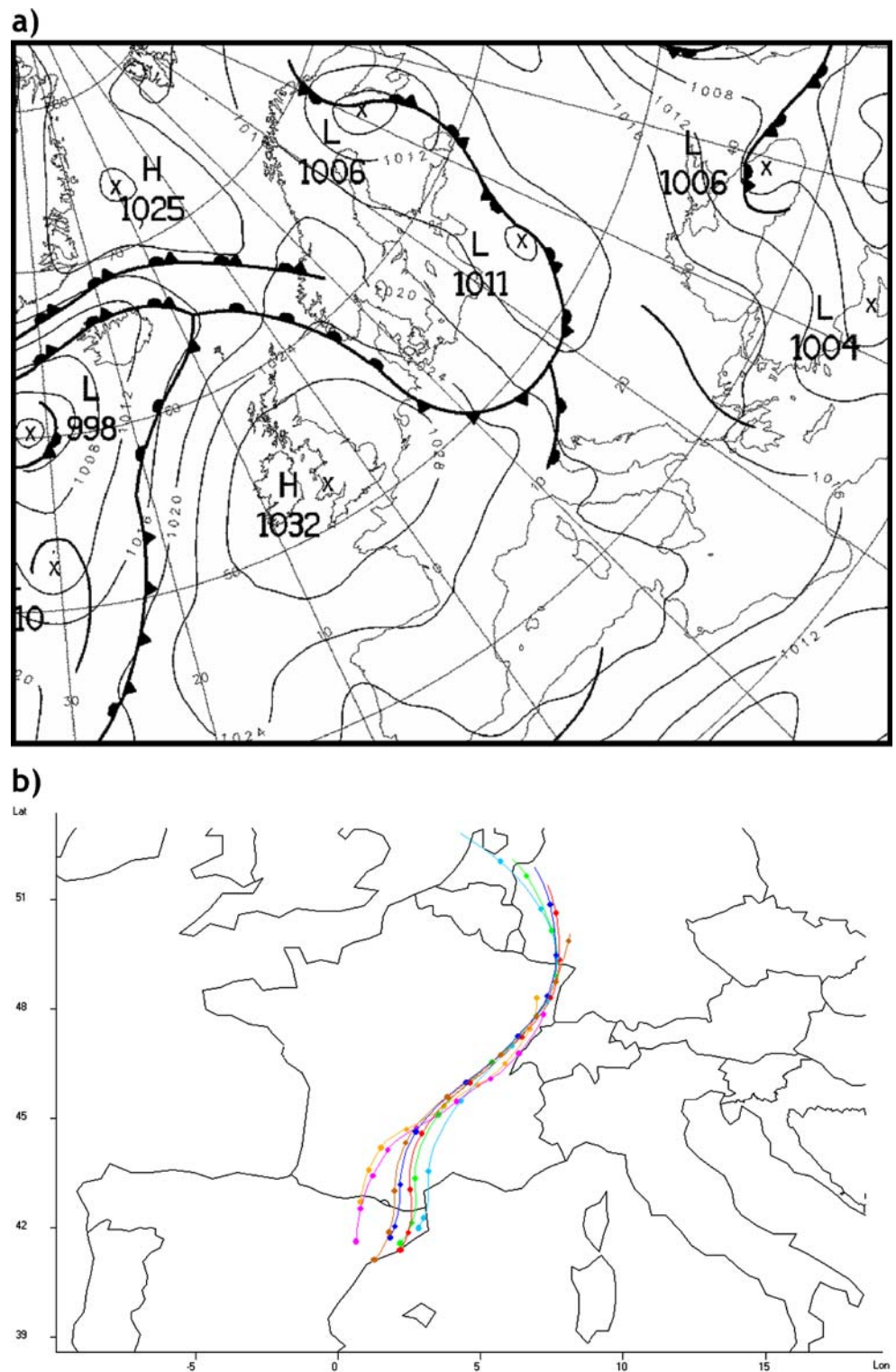
Episode of 16 and 17 May 2004

During the 16 and 17 May 2004, all of the Catalan monitoring stations recorded a very large pollen peak (Fig. 2), with values up to 90 grains/m³, representing the highest mean daily concentrations in the whole 23-year record. The synoptic situation during this episode was characterised by a high pressure nucleus over the British Isles and a low pressure centre to the east of the Scandinavian Peninsula (Fig. 3a). This resulted in a synoptic circulation with prevailing south-west winds from central Europe to the Iberian Peninsula. The Hysplit back trajectories for this event showed that the air mass followed the corridor between the British high and the eastern Scandinavian low, linking central Europe (SW Germany, NE France, western Switzerland) with Catalonia (Fig. 3b). The pathway drawn by these back trajectories crossed the Pyrenees range at a region where it reaches altitudes of 3,000–3,500 m. Therefore, the Pyrenees could act as a barrier for the transport. To study this aspect further, a more refined analysis was performed using the MM5 mesoscale model. The simulation started on the 15 May at 0000 hours UTC, and continued for 3 days. Atmospheric variables were obtained every hour. A comparison between the trajectories obtained from the MM5 smallest domain results and the hourly pollen distribution in the study stations in Catalonia (Fig. 5) allowed a more refined interpretation of

Table 5 Contingency tables to test the null hypothesis of independence of *Fagus* pollen peaks and the influx of European air masses (inferred from Hysplit back trajectories) at the monitoring sites of Girona and Barcelona for the two years of highest *Fagus* pollen in the 1983–2007 record

		European	Non European	Total
Girona 2004	Pollen peak	14	2	16
	No pollen peak	30	26	56
	Total	44	28	72
		$\chi^2=6.03$; $P=0.014$		
Barcelona 2004	Pollen peak	9	0	9
	No pollen peak	35	28	63
	Total	44	28	72
		$\chi^2=6.55$; $P=0.0105$		
Girona 2006	Pollen peak	6	5	11
	No pollen peak	14	47	61
	Total	20	52	72
		$\chi^2=4.64$; $P=0.031$		
Barcelona 2006	Pollen peak	3	3	6
	No pollen peak	17	49	66
	Total	20	52	72
		$\chi^2=2.03$; $P=0.155$		

Fig. 3 **a** Sea level pressure analysis at 0000 hours UTC on 16 May 2004. **b** Hysplit back trajectories on 17 May 2004 at all studied stations in Catalonia. Hysplit isentropic 96-h back-trajectories at 60-min time steps at 1,500 m a.s.l., starting at 1200 hours UTC from the coordinates of each monitoring site. Available at <http://www.arl.noaa.gov/ready/hysplit4.html> (Draxler and Rolph 2003)



pollen arrival in the area. During 15 May there was a heterogeneous air mass flux, and only one station (Girona) received northerly winds (Fig. 4a). At that point, the pollen was barely present at any of the monitoring stations. The air flux started to be more organised on 16 May. At 0000, 0600 and 1200 hours

UTC, all the stations showed an influx of northern air masses (Fig. 4b–d). Simultaneously, the hourly distribution showed the first appearance of pollen at all stations (Fig. 5d–f). The situation changed between 1200 and 1800 hours UTC (Fig. 4e), when only Girona received northern air masses, the other stations being disconnected from the

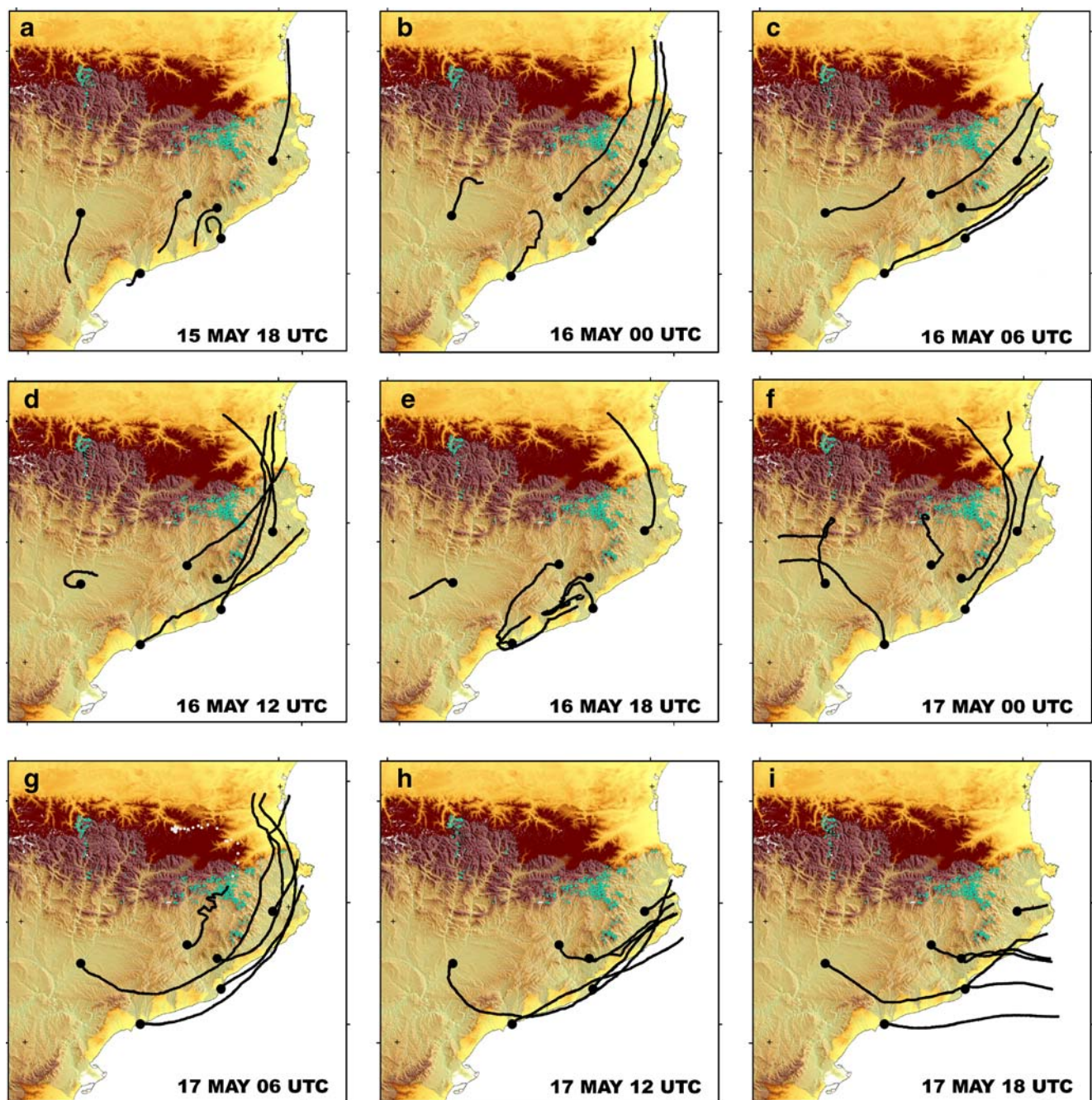


Fig. 4 Back trajectories calculated with the MM5 model simulation at the Catalan stations (<http://www.mmm.ucar.edu/mm5/mm5-home.html>). Blue dots indicate inventory sites where *Fagus* is present [data

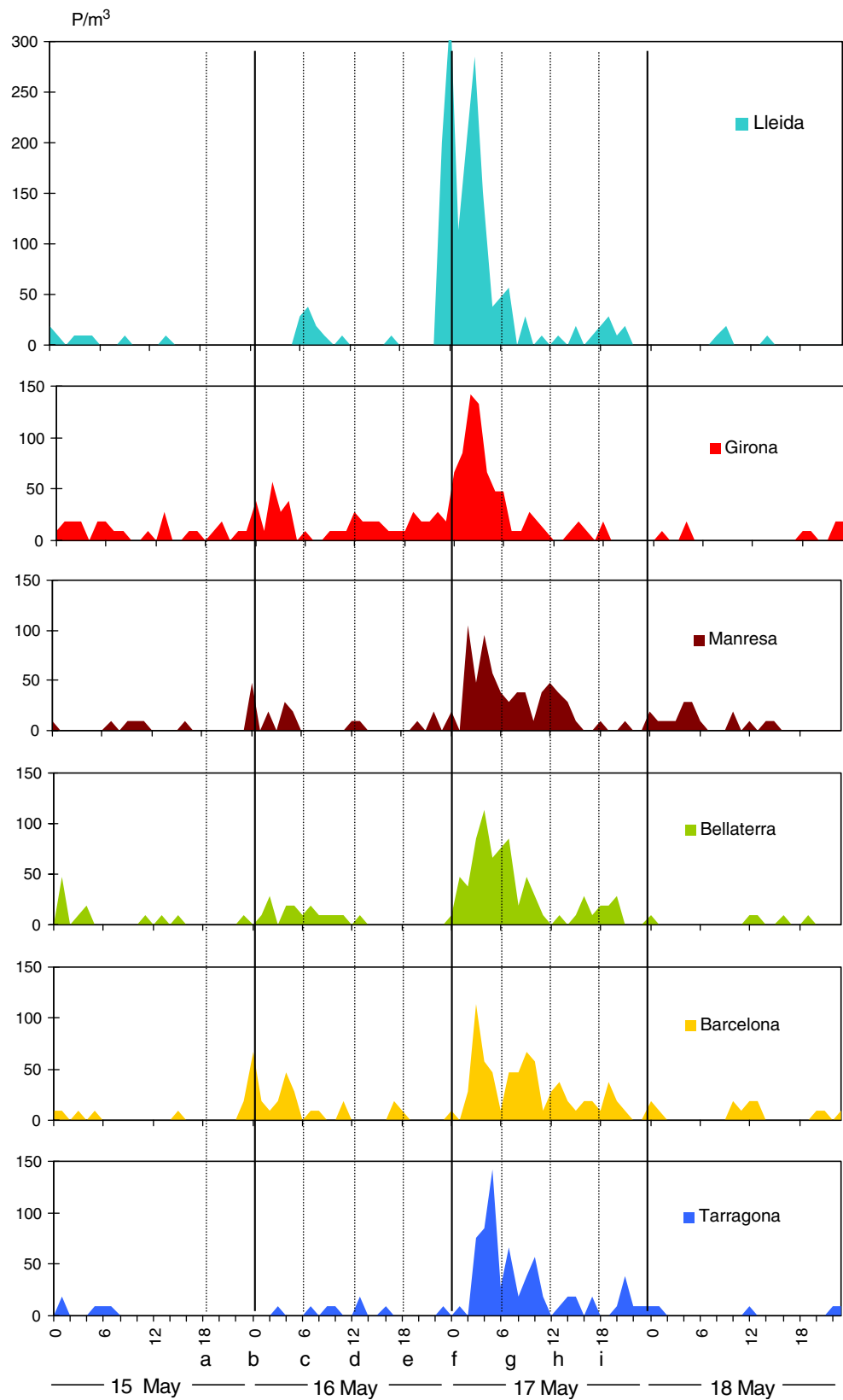
from the IEF (Inventari Ecològic i Forestal de Catalunya, <http://www.creaf.uab.es/iefc/>) and IFN2 (Inventario Forestal Nacional, <http://www.mma.es/portal/secciones/biodiversidad/inventarios/ifn>)]

northern flux (Fig. 4e). However, at 0000 UTC on 17 May (Fig. 4f), the air flux was again from the northeast, reaching a homogeneous orientation in all stations on at 0600 hours UTC (Fig. 4g). This synoptic situation produced the maximum amount of pollen in all stations, as can be seen from the hourly records (Fig. 5g,h). Afterwards, the situation changed towards an easterly wind pattern from the Mediterranean Sea, which was clearly established at 1800 hours UTC (Fig. 4i). Pollen

was still found in the atmosphere, although decreasing rapidly (Fig. 5).

Besides regional features and regional patterns of wind movement, the mesoscale model MM5 takes into account the local scales of the atmosphere. It should be noted that the northern European fluxes simulated with MM5 showed a particular characteristic that could not be distinguished with Hysplit. For the event on 17 May 2004, Hysplit modelled the trajectories straight back

Fig. 5 Mean hourly pollen concentrations (in pollen grains/m³) at the Catalan stations from 15 May 2004 at 0000 hours UTC to 18 May at 2300 hours UTC. Letters on the x-axis refer to parts a–i in Fig. 4 to illustrate the correspondence of pollen abundance and the transport modelled with MM5



from the north (Fig. 3b), while the MM5 model added detail by showing a consistent flow through the easternmost Pyrenean extreme at the Alberes region (500 m a.s.l.), an easier pass than the 3,000–3,500 m a.s.l. altitudes of the central Pyrenees. Therefore, these two back trajectory models contained complementary information: long-range transport, or the provenance source, was best inferred with Hysplit, which suggested probable source forests in the Jura (French–Swiss border), the Vosges (NE France), and the Schwarzwald (SW Germany). On the other hand, MM5 added value by modelling transport at the regional scale, being able to trace the path through the easternmost Alberes pass.

Source areas

Application of the receptor model to pollen data from the period 1997–2006 enabled identification of the probable source regions of *Fagus* pollen. The model suggests a broad provenance area between the north of Italy, Switzerland, northeastern France and southwestern Germany—a region extensively covered by beech forests (Fig. 6). It should be noted that the outstanding event of 16–17 May 2004 was also back-traced to this region. Several studies have shown that the source–receptor methodologies are adequate tools for identifying far distant source areas (Charron et al. 1998).

Contribution to phylogeography and palaeopalynology

The results obtained in this study show that *Fagus* pollen can occasionally be transported very far from its source forests. This fact may affect other disciplines, such as palae-

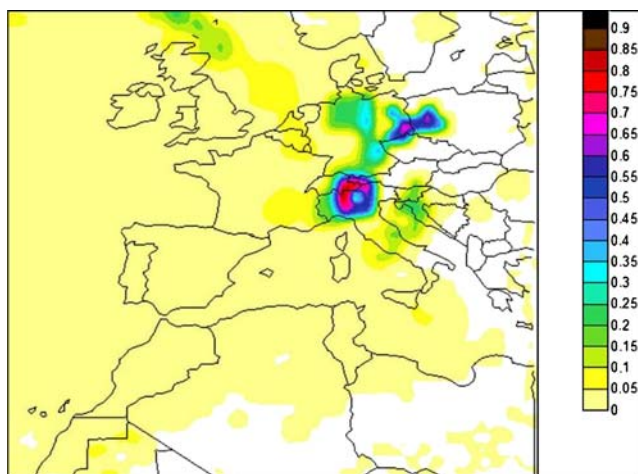


Fig. 6 Areas contributing to *Fagus* pollen concentrations, inferred from a source–receptor model applied to spring pollen counts (1 April to 30 June) at the Catalan stations for the period 1997–2007. See text for details

opalynology and phylogeography. For example, Bradshaw (2004), among others, considered that *Fagus* pollen does not travel far from its source and that relative abundance of pollen is a relatively unbiased reflection of the abundance of trees in the surrounding forests. Our results indicating long range transport suggest that *Fagus* distribution maps elaborated from paleopalynological evidence could in some cases over-represent these local forests.

As for phylogeography, Magri et al. (2006) evaluated the genetic consequences of long-term survival of *Fagus* in refuge areas and the postglacial spread from palaeobotanical data (400 fossil pollen sites and 80 plant-macrofossil sites) and genetic data (450 and 600 modern populations analysed for chloroplasts and nuclear markers, respectively). In Angiosperms, chloroplast markers are inherited only maternally (Liepelt et al. 2002), so we refer only to the results published by Magri et al. (2006) on isozyme data (nuclear markers). These results established a geographical distribution of isozyme groups throughout the Pyrenees, France and Catalonia that are better explained by episodes of long-range transport of *Fagus* pollen, such as those shown in this paper. The problems traditionally faced in species delimitation and phylogeny reconstruction may be due in part to a combination of weak reproductive barriers and the large distances that can be covered by genetic information as a result of wind pollination (Schmidt-Lebuhn et al. 2007).

Conclusions

This study shows that beech pollen dispersal can cover thousands of kilometres. Hysplit back trajectories and the MM5 model were useful for describing pollen transport, and the two models provided complementary information. Long-range transport and probable source areas in central Europe were best described with Hysplit back trajectories and its associated source–receptor model, while MM5 allowed for more detail on the local scale, being able to trace the flow path through the Pyrenean range.

The fact that *Fagus* pollen peaks appeared simultaneously in different stations across the Catalan geography indicated a broad-scale phenomenon, dominating over local influences. The application of a source–receptor model showed that the area in Europe from north Italy to central Germany, rather than the Pyrenean region, was the most probable area of emission responsible for the pollen peaks collected in Catalonia. This region is covered by extensive beech forests. Detailed study of the event of 17 May 2004, when the highest pollen levels in the 23 year record were observed, showed that the provenance area was most likely in the Vosges (NE France) or the Schwarzwald (SW Germany).

This long-range transport could have consequences for the understanding of modern pollen genetic diversity, and give some clues to future interpretations of fossil pollen diagrams. Also, because of the reported allergenicity of *Fagus* pollen, understanding of pollen dispersal is urgently required by European health care systems.

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