



Modern pollen rain in Canary Island ecosystems and its implications for the interpretation of fossil records



Lea de Nascimento^{a,*}, Sandra Nogué^{b,c}, Silvia Fernández-Lugo^a, Javier Méndez^a, Rüdiger Otto^a, Robert J. Whittaker^{d,e}, Kathy J. Willis^{b,c}, José María Fernández-Palacios^a

^a Island Ecology and Biogeography Group, Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUNETSPC), Universidad de La Laguna (ULL), Avda. Astofísico Francisco Sánchez s/n, La Laguna 38206, Canary Islands, Spain

^b Oxford Long-term Ecology Laboratory, Biodiversity Institute, Department of Zoology, University of Oxford, Tinbergen Building, South Parks Road, Oxford, OX1 3PS, United Kingdom

^c Department of Biology, University of Bergen, Post Box 7803, N-5020, Norway

^d Conservation Biogeography and Macroecology Programme, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, United Kingdom

^e Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

ARTICLE INFO

Article history:

Received 10 December 2013

Received in revised form 8 August 2014

Accepted 5 November 2014

Available online 20 November 2014

Keywords:

Canary Islands
Elevation gradient
Laurel forest
Palaeoecology
Pollen
Vegetation

ABSTRACT

Vegetation history in the Canary Islands, one of the most biodiverse regions within Europe, has recently and for the first time, been the subject of palaeoecological studies. The interpretation of fossil records may be limited by several uncertainties regarding how well the different vegetation types are represented in the pollen rain. In this study we address this key knowledge gap within Canarian vegetation science, taking the island of Tenerife as a model. Based on quantitative and qualitative data we analysed pollen–vegetation relationships to test whether different vegetation types can be discriminated by means of their pollen rain composition, to identify under- and over-represented taxa, and to test the match between modern pollen rain and fossil pollen assemblages. We found clear differences in pollen composition and abundance among major Canarian vegetation types. We also identified good indicator taxa of the local occurrence of their source plants by their high fidelity and low dispersibility index scores. Extra-regional types (taxa without potential source plants in the Canary Islands) were not detected in our traps. However, several important floristic elements are either over-represented (*Pinus*, *Morella* and *Ericaceae* trees, *Chenopodiaceae*, *Poaceae*, *Rumex* and *Urticaceae* herbs and shrubs) or under-represented (*Lauraceae* trees, *Fabaceae* and *Euphorbia* shrubs). Results indicate that pollen composition is a good reflection of vegetation in Canarian ecosystems and can be used effectively to reconstruct past environments.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

An essential principle of fossil pollen analysis is that the pollen rain input to a site is a function of the vegetation composition around the site and therefore, the proportion of pollen found at any level of a sedimentary sequence depends on the abundance of parent plants existing in the locality at the time of deposition (Birks and Birks, 1980). However, the pollen–plant abundance relationship is complex and depends on species-specific variation in pollen productivity, transport mechanisms, deposition and preservation (Bradshaw and Webb, 1985; Faegri and Iversen, 1989). It has long been acknowledged that this introduces uncertainty into the interpretation of fossil pollen

sequences. Hence, much effort has been put into developing tools for quantitative reconstruction of past vegetation from fossil pollen assemblages (Fagerlind, 1952; Davies, 1963; Webb et al., 1978; Jacobson and Bradshaw, 1981; Prentice, 1985; Sugita, 1993).

The analysis of modern pollen rain is a necessary first step in understanding pollen–plant relationships. Previous studies of modern pollen rain on islands worldwide have shown the capacity to distinguish the main vegetation types from pollen assemblages (e.g. Arctic and subantarctic islands (McGlone and Moar, 1997; Lozhkin et al., 2001), temperate islands (Deng et al., 2006; Fletcher and Thomas, 2007a), Mediterranean islands (Fall, 2012), tropical and subtropical islands (Dodson, 1982; Collins and Bush, 2010)).

Insular pollen rain composition may show varying degrees of influence of external pollen sources, depending on island size, isolation, plant composition of source areas (nearby islands and continents) and prevailing wind currents (Salas, 1983; Gajewski, 1995; McGlone and Moar, 1997; Lozhkin et al., 2001; Collins and Bush, 2010; van der Knaap et al., 2012; and see Jackson and Dunwiddie, 1992 for theoretical overview). Within islands, topoclimatic gradients can be very strong,

* Corresponding author. Tel.: +34 922318669.

E-mail addresses: leadenas@ull.es (L. de Nascimento), sandra.noguebosch@zoo.ox.ac.uk (S. Nogué), sfdezlu@ull.es (S. Fernández-Lugo), jmendezh@ull.es (J. Méndez), rudiger.otto@gmail.com (R. Otto), robert.whittaker@ouce.ox.ac.uk (R.J. Whittaker), Kathy.Willis@zoo.ox.ac.uk (K.J. Willis), jmferpal@ull.es (J.M. Fernández-Palacios).

with implications for pollen mixing amongst different major ecosystem types within short horizontal distances. In general, this involves upwards transport between vegetation zones (Faegri and Iversen, 1989; Cañellas-Boltà et al., 2009; Niemann et al., 2010), although local and regional wind circulation patterns may also be important to pollen mixing across an island and to pollen transport from external sources (Izquierdo et al., 2011). The problem is accentuated in treeless situations (grasslands and shrublands) where pollen production is usually low and distant pollen rain increases in importance (Dodson, 1976; Deng et al., 2006; Fletcher and Thomas, 2007a; Collins and Bush, 2010).

Although Izquierdo et al. (2011) have undertaken an analysis of potential long-distance sourcing of pollen rain on Tenerife there have been no previous studies of modern pollen rain in relation to vegetation for the Canary Islands, presenting constraints on the interpretation of fossil pollen evidence from these islands. Two recent palaeo-ecological studies from former lakebed sites within the evergreen monteverde forest have recorded marked changes in species composition within the last 9600 years in response to climatic and anthropogenic drivers. On the island of La Gomera, abundantly represented hygrophilous trees were replaced around 5500 years ago by taxa of the monteverde forest, which was interpreted as indicating a shift towards drier conditions (Nogué et al., 2013). On Tenerife, in which the record extends only as far back as 4700 years ago, a major shift in forest composition was initiated around 2000 years ago, with the decline and eventual disappearance of *Quercus* (oak) and *Carpinus* (hornbeam) from the pollen record, implicating the first human colonists of the islands as major drivers of vegetation change (de Nascimento et al., 2009). These intriguing findings nonetheless leave open many questions about the role of humans and climate and the climate-sensitivity of the vegetation of these islands, in part arising from the lack of knowledge of modern vegetation–pollen relationships within the Canaries.

Within both sequences, Lauraceae pollen was largely absent from the fossil records, despite species of this family having a prominent role in the best-developed stands of monteverde forest historically. In contrast, *Morella* and *Erica* pollen types were well represented in both palaeo-sequences. Within the Canaries today, stands of *Morella-Erica* woody heath (*Morella faya* and *Erica* spp.) form a low canopied forest on exposed areas but also constitute the pioneer phase to the evergreen laurel forest in which Lauraceae (e.g. *Laurus*, *Apollonias*, *Ocotea* and *Persea*) are characteristic and prominent components (del Arco et al., 2010). Finer resolution interpretation of palaeo-sequences for these islands therefore requires insight into the representation of these taxa in the modern pollen rain. Another unresolved question was how to interpret pollen characteristic of other major vegetation types within the cores. For instance, pollen characteristic of the elevationally adjacent Canarian forest ecosystems, thermophilous woodlands (lower elevation) and pine forests (higher elevation), were detected in both sedimentary sequences, but pollen indicative of the coastal and summit scrubland systems were lacking. Finally, the estimation of pollen arrival from nearby continental areas would help to clarify the significance of long distance pollen transport in our records, paying particular attention to those pollen types that can be distinguished definitively from the Canarian native types.

We present herein the first study of pollen–vegetation relationships for the Canary Islands, analysing modern pollen content of artificial traps located across an elevational gradient ranging from 10 to 2250 m above sea level (a.s.l.), thus including a representation of major vegetation types (forests and shrublands) on the island of Tenerife (the highest Canarian island). We aim to improve the interpretation of pollen–plant community relationships in the Canaries by answering the following specific questions: 1) How well can we distinguish vegetation types from their pollen rain? 2) Within vegetation types, is there over or under-representation of certain key taxa? 3) What is the contribution of long-distance transported pollen in the pollen rain? And finally, 4) how well do past pollen assemblages resemble present communities?

2. Material and methods

2.1. Study site

Tenerife is the highest (3717 m a.s.l.) and biggest (2034 km²) island in the Canarian Archipelago. The major vegetation types are arranged in elevational belts, including different forest ecosystems (thermophilous woodland, monteverde and pine forest) distributed across the mid-elevations, whereas shrubland communities occupy both lowlands (coastal shrubland) and summit (summit scrub) (Fernández-Palacios and de Nicolás, 1995; del Arco et al., 2010). The strong influence of trade winds over the northern flank of the island is largely responsible for contrasting climate zonations between the windward and leeward elevations. The leeward (southern) side is drier, so that the monteverde zone is largely absent, allowing for the expansion of the more xeric ecosystems (pine forest and thermophilous woodland). The gradient covered within our sampling reflects wide climatic variability, ranging from an average temperature of 18–22 °C in the lowlands to 3–11 °C in the summit regions. Annual precipitation is highest in the mid-elevations (300–800 mm) and can reach up to 1300 mm under the influence of the ‘sea-of-clouds’ on the windward flank, whereas both summit (500 mm) and lowlands (100–300 mm) are much drier (del Arco et al., 2010). The driest season is the summer.

The current distribution of the main vegetation types is not only climatically restricted but has been greatly shaped by human activities (del Arco et al., 2010) so that contemporary vegetation communities may provide only partial analogues for past pre-colonization communities, even to the extent of significant canopy species being lost from the native vegetation altogether (de Nascimento et al., 2009). The pine forest was historically greatly reduced but currently occupies around half the area it is estimated to have occupied prior to human colonization, mainly thanks to mid-20th Century reforestation efforts. The thermophilous woodland was historically the most intensively used zone and only an estimated 2% remains. The monteverde formation was once reduced to around 10% of its hypothesised original extent but has recently expanded into abandoned agricultural land, reaching around 30% of its estimated former extent. Coastal shrubland is currently being transformed at the fastest rates by human settlement and construction pressure, and is estimated to have been reduced to approximately 33% of its original extent. By contrast, the summit scrub covers perhaps 90% of its natural area of distribution and much of it has been under protection since the establishment of the National Park in 1954 (del Arco et al., 2010).

Coastal shrubland (COAS) represents the African element of the Canarian flora and covers extensive areas of the lowlands (0–500 m a.s.l.). This species rich formation is dominated by several *Euphorbia* species, on Tenerife mainly represented by *Euphorbia balsamifera*, *E. lamarckii* and *E. canariensis*, together with other accompanying species, notably *Kleinia neriifolia*, *Neochamaelea pulverulenta*, *Periploca laevigata* and *Schizogyne sericea*.

Immediately above (300–900 m a.s.l.), small fragments of thermophilous woodland (THER) appear. Of Palaeo-Mediterranean origin, these woodlands do not constitute a uniform community, but instead comprise different communities of shared distributional origin and climatic affinities. Often the remnant patches are characterized by a single prominent tree species, typically *Juniperus turbinata*, *Olea cerasiformis*, *Pistacia atlantica* or *Phoenix canariensis*. In the understory there are plenty of herbaceous and shrub species, making this forest one of the most diverse and endemic-rich vegetation types on the island (Fernández-Palacios et al., 2008; Otto et al., 2012).

Located mostly on the windward flank and spanning a broad elevational band (350–1500 m a.s.l.), the monteverde is a broadleaved evergreen cloud forest formation relictual from the Tethyan-Tertiary flora (Fernández-Palacios et al., 2011). It comprises two widely recognised communities: the laurel forest and *Morella-Erica* woody heath. Common co-dominants of the so-called laurel forest (LAUR)

include trees of the family Lauraceae, specifically *Apollonias barbuja*, *Laurus novocanariensis*, *Ocotea foetens* and *Persea indica*. The woody heath, dominated by *Erica arborea*, *E. platycodon* and *Morella faya*, characterises exposed areas within the monteverde domain (windy or steep slopes and high elevations) and also comprises the pioneer phase following major disturbances (such as clear-felling or volcanic disruption) to the laurel forest. Other trees participating in the cloud forest zone are: *Ilex* spp., *Picconia excelsa*, *Prunus lusitanica*, *Rhamnus glandulosa*, and *Viburnum rigidum*.

Pine forest (PINE) is the highest forest ecosystem (900–2200 m a.s.l.) and thus also forms the upper treeline. Poor in species, this forest is characterized by a dominant tree species, the palaeoendemic *Pinus canariensis*, which was formerly distributed throughout the Mediterranean basin (Klaus, 1989). Among the few species occurring in the understory are *Adenocarpus* spp., *Chamaecytisus proliferus*, and *Cistus* spp.

Finally, in the highest elevations (2200–3250 m a.s.l.) a summit scrub formation (SUMM) occurs, which shares Mediterranean and North-African affinities. The most prevalent species currently are *Adenocarpus viscosus*, *Descurainia bourgeauna*, *Pterocarpus lasiospermus* and *Spartocytisus supranubius* (del Arco et al., 2006). The presence of this wide array of vegetation formations on Tenerife makes the island a good model for the study of pollen–vegetation relationships across the rest of the Canarian archipelago.

2.2. Field and laboratory methods

Based on our published accounts and own knowledge of the vegetation of the island, we selected well preserved areas to represent these major vegetation types (Table 1, Fig. 1a–e). Sampling sites were then randomly located within each area, excluding inaccessible zones. THER

plots were specifically located in some of the scarce and small remnants, resulting in a scattered distribution of sites. These fragments were selected with the aim of providing a good representation of the different communities in the THER zone, i.e. *Olea cerasiformis*, *Pistacia atlantica*, and *Juniperus turbinata* woodlands, and the Canarian palm (*Phoenix canariensis*) and willow (*Salix canariensis*) community. Traps were located in six plots within each vegetation type, equally distributed between windward and leeward (except for SUMM where no clear distinction can be made as to the exposition), making a total of 30 plots. In the centre of each plot four traps were set up, linearly spaced at intervals of two meters to avoid unbalanced pollen rain caused by spatial variability within plots. The standard plot size used was 400 m² (20 × 20 m) except for LAUR sites where bigger plots of 2500 m² (50 × 50 m) were needed to get realistic estimates of the forest composition. We used artificial traps as a consistent sampling method in all localities rather than moss polsters because of the scarcity of mosses in some ecosystems. The use of Behling traps has been recommended in open ecosystems where drought and strong radiation are common (Jantz et al., 2013). In our study, this type of trap worked well and proved its efficacy under markedly different climatic conditions (from snow or heavy rain to high insolation). Based on Behling et al. (2001), traps were made of plastic tubes of 100 cm³, filled with 10 cm³ of glycerine, covered with 1 mm nylon mesh, and fixed to an iron bar at 10 cm above the surface (Fig. 1f). All traps remained in the field for 16 months, April 2010–July 2011, covering two consecutive springs.

Pollen preparation involved the addition of exotic *Lycopodium* spores as a marker, sieving through a mesh of 150 microns to remove plant remains, a brief treatment of two minutes with acetolysis mixture to eliminate polysaccharides, then dying with aqueous safranin and dehydrating with *tert*-Butyl alcohol, and finally preserving and mounting samples in silicone oil (Bennett and Willis, 2001). A minimum count of

Table 1

Main characteristics of plots included in the study of modern pollen rain on Tenerife, Canary Islands.^a

Plot	Location	Vegetation	Elevation (m)	Asp.	UTMX	UTMY	Natural Protected Area
CW1	Punta de Teno	COAS	48	W	312445	3136651	Teno RP
CW2	Punta de Teno	COAS	65	W	312527	3136650	Teno RP
CW3	Punta de Teno	COAS	77	W	312558	3136674	Teno RP
CL1	Punta de La Rasca	COAS	13	L	333835	3098455	Malpaís de La Rasca ENR
CL2	Punta de La Rasca	COAS	22	L	333536	3098550	Malpaís de La Rasca ENR
CL3	Punta de La Rasca	COAS	20	L	333866	3098630	Malpaís de La Rasca ENR
TW1	Afur	THER	316	W	378389	3159912	Anaga RP
TW2	Buenvista	THER	326	W	319777	3138289	Teno RP
TW3	Afur	THER	345	W	378433	3160090	Anaga RP
TL1	El Cercado	THER	217	L	381902	3156724	Anaga RP
TL2	Laderas de Güimar	THER	529	L	360961	3130537	Corona Forestal NP
TL3	Montaña de Tejina	THER	776	L	327339	3119523	Montaña de Tejina NM
LW1	El Moquinal	LAUR	773	W	371922	3157396	Anaga RP
LW2	El Moquinal	LAUR	793	W	372138	3157386	Anaga RP
LW3	El Moquinal	LAUR	810	W	371884	3157267	Anaga RP
LL1	Monte de Aguirre	LAUR	885	L	375777	3156943	Anaga RP
LL2	Monte de Aguirre	LAUR	953	L	375407	3157012	Anaga RP
LL3	Monte de Aguirre	LAUR	962	L	376003	3156950	Anaga RP
PW1	La Esperanza	PINE	1139	W	363974	3144554	Las Lagunetas PL
PW2	La Esperanza	PINE	1150	W	363843	3143913	Las Lagunetas PL
PW3	La Esperanza	PINE	1290	W	363435	3143075	Las Lagunetas PL
PL1	Vilaflor	PINE	1179	L	338445	3118107	Corona Forestal NP
PL2	Vilaflor	PINE	2014	L	335575	3119610	Corona Forestal NP
PL3	Vilaflor	PINE	2061	L	337433	3119270	Corona Forestal NP
SI1	Izaña	SUMM	2163	-	347955	3131952	Teide NatP
SI2	Izaña	SUMM	2192	-	352207	3132287	Teide NatP
SI3	Izaña	SUMM	2255	-	349087	3131805	Teide NatP
SC1	Las Cañadas	SUMM	2097	-	344392	3124967	Teide NatP
SC2	Las Cañadas	SUMM	2198	-	342481	3123200	Teide NatP
SC3	Las Cañadas	SUMM	2243	-	340631	3125371	Teide NatP

^a Name of plots indicate vegetation type (first letter), aspect (Asp.) or location in the case of summit plots (second letter) and elevational position (1–3 from lowest to highest elevation). Abbreviations stand for: vegetation type (COAS = coastal shrubland, THER = thermophilous woodland, LAUR = laurel forest, PINE = pine forest, SUMM = summit scrub), aspect (W = windward, L = leeward), location of summit plots (I = Izaña, C = Las Cañadas), and category of protected area (ENR = Especial Natural Reserve, NM = Natural Monument, NP = Natural Park, NatP = National Park, PL = Protected Landscape, RP = Rural Park).

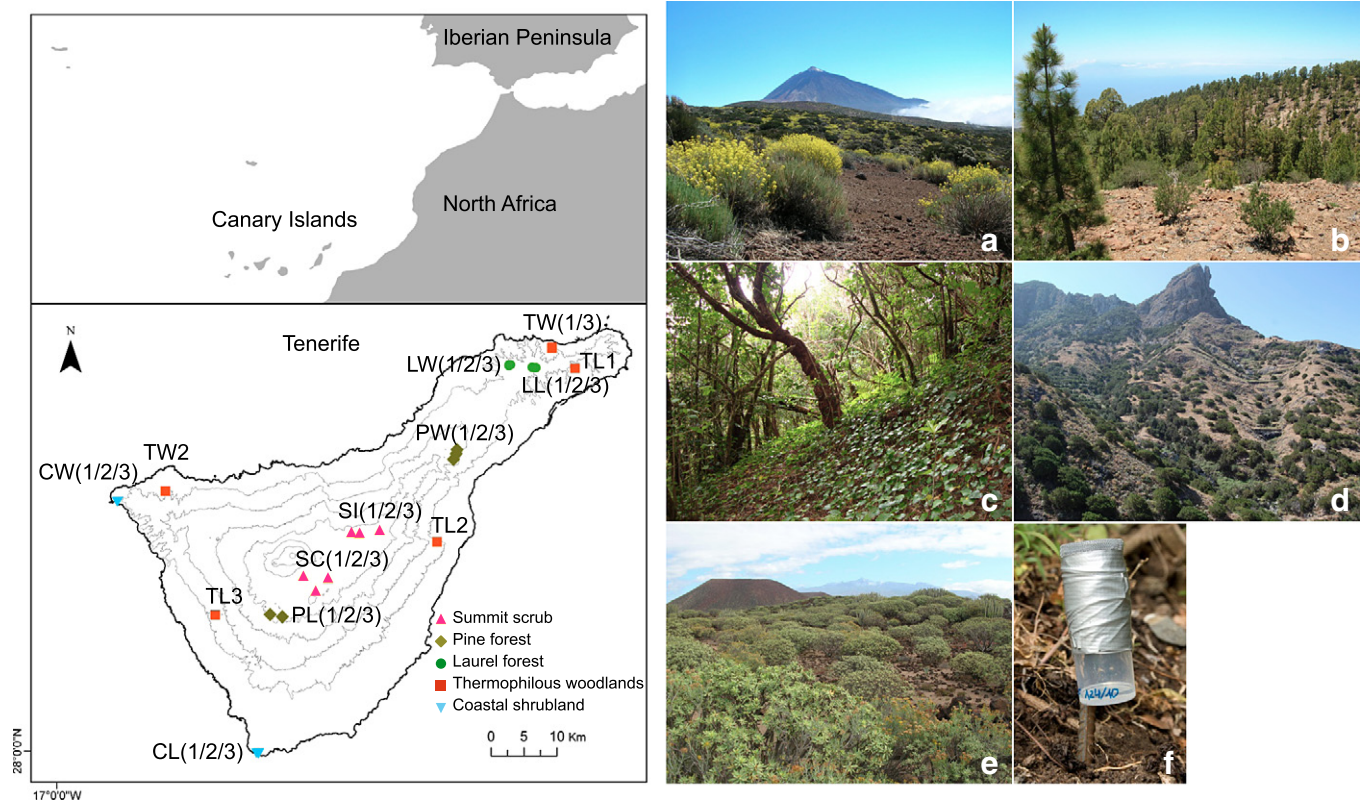


Fig. 1. Location of plots used for pollen rain and vegetation monitoring in Tenerife (Canary Islands) for the period April 2010–July 2011. Names of plots indicate vegetation type (S = summit scrub, P = pine forest, L = laurel forest, T = thermophilous woodland and C = coastal shrubland) and aspect (W = windward, L = leeward) or location for summit plots (I = Izaña, C = Las Cañadas). On the right are images of the different vegetation types: summit scrub (a), pine forest (b), laurel forest (c), thermophilous woodland (d), coastal shrubland (e), and an example of a pollen trap (f).

400 pollen grains (i.e. a minimum of 100 grains per trap) was obtained for each plot, including fern spores in the pollen sum. Identification was based on the reference pollen collection held at the Ecology Laboratory, University of La Laguna, and the photographs in Reille (1992, 1995, 1998).

Plant cover for each species was measured by means of the line intercept method (Canfield, 1941) along five parallel transects of 20 m, spaced at regular intervals within every plot. Species present in the plot but not intercepted by any transect were also recorded. Additionally, basal area of arboreal species was estimated by measuring the diameter at breast height (DBH) for every stem over 2.5 cm DBH in all forest plots. Compared to plant species identification, pollen usually presents lower taxonomic resolution, in most cases only reaching genus or family level (or, in the case of ferns, division level). To facilitate comparative data analyses plant species recorded in the vegetation survey were grouped into higher taxonomic levels to match their corresponding pollen types (see Table S.1, Supplementary data).

2.3. Data analyses

Both qualitative (based on pollen and plant presence/absence data) and quantitative (based on pollen percentage, plant cover percentage and basal area) assessments were applied in the analysis of pollen–vegetation relationships. Initially, ordination analyses were used to explore differences in pollen composition (based on pollen percentage) and its relationship with vegetation (plant cover and basal area) among vegetation types. Each vegetation type was then considered alone to examine similarities between pollen and vegetation composition. Detrended correspondence analysis (DCA) was used when the gradient was longer than 4 standard deviation units; otherwise we used principal components analysis (PCA), assuming predominantly linear responses

of species to gradients (Lepš and Šmilauer, 2003). All ordination analyses were generated using CANOCO for Windows 4.5 (ter Braak and Šmilauer, 2002).

In a subsequent step we tested for significant differences in pollen composition among vegetation types ($p < 0.01$) by means of permutational analysis of variance (PERMANOVA) based on Bray–Curtis distance matrices (Anderson et al., 2008), assigning vegetation type as a fixed factor. Additionally, for each vegetation type, differences between pollen and vegetation composition were tested with PERMANOVA ($p < 0.01$), with pollen and plant cover being levels of the fixed factor. Plot was selected as a random nested factor in both PERMANOVA designs, and pair-wise comparisons were undertaken using t -tests ($p < 0.01$), applying Monte Carlo correction when needed. Finally, similarity percentage analysis (SIMPER) was used as a quantitative measure of over- and under-representation in the pollen signal, to show which taxa contributed to dissimilarities between pollen and vegetation composition. PRIMER 6 with PERMANOVA + software was used to perform permutational ANOVA and SIMPER analyses (Anderson et al., 2008). When pollen percentage and vegetation data (either plant cover or basal area) were analysed in the same data set square root transformation was applied prior to both ordination and PERMANOVA analyses.

Fidelity and dispersibility indices were calculated for individual taxa based on pollen and plant presence/absence data (Davis, 1984; McGlone and Meurk, 2000). Fidelity was calculated as the percentage of sites (plots) where a given taxon coincides both in pollen and vegetation, as a function of those sites in which the taxon is present in the vegetation. Dispersibility was calculated as the percentage of sites where a given taxon is only recorded in the pollen rain, as a function of those sites in which the taxon is absent from the vegetation. Taxa with less than 5% in either pollen or plant cover percentages at any sample were excluded from these calculations. After plotting fidelity versus

dispersibility indices, pollen types were grouped into five main groups based on similarity of values (Deng et al., 2006; Fletcher and Thomas, 2007b; Fall, 2012).

DCA and PCA were also used to explore similarities in composition among modern pollen rain and fossil pollen content in the samples of two sedimentary sequences from La Laguna in Tenerife (4700–400 cal. yr BP) and Laguna Grande in La Gomera (9600–0 cal. yr BP). We compared pollen composition of different vegetation types and pollen zones, as defined for each pollen diagram (de Nascimento et al., 2009; Nogué et al., 2013), using a one-way PERMANOVA ($p < 0.01$) based on a Bray–Curtis distance matrix. Average similarity between groups was obtained after pair-wise comparisons using the t -test ($p < 0.01$), applying Monte Carlo correction when necessary.

Modern pollen percentages of selected taxa, together with arboreal (AP) versus non-arboreal pollen (NAP) ratio, and pollen influx (grains $\text{cm}^{-2} \text{year}^{-1}$), were represented along the elevational gradient, using Pimpoll 4.26 (Bennett, 2008).

3. Results

3.1. Pollen rain composition

The vegetation surveys provided a total of 236 species, while 99 pollen types were recorded in the modern pollen samples (Table S.1., Supplementary data). The elevational gradient in vegetation was clearly reflected in the pollen trap data, with AP peaking in the mid-elevation belt, but also with some striking variation within zones (COAS 0%, THER 18–58%, LAUR 82–98%, PINE 20–93%, SUMM 2–33%) (Fig. 2). Differences in pollen influx were especially marked within SUMM, with values ranging from 4400 to 50700 grains $\text{cm}^{-2} \text{year}^{-1}$. The highest mean pollen influx across sites was found for the LAUR zones, with values per site varying between 14800 and 36000 grains $\text{cm}^{-2} \text{year}^{-1}$. In both PINE and THER, pollen influx showed lower ranges of variation, with 4500–13700 and 4700–25600 grains $\text{cm}^{-2} \text{year}^{-1}$, respectively. The lowest pollen influx was for the COAS samples, which varied between 1000 and 2800 grains $\text{cm}^{-2} \text{year}^{-1}$ across the six sites.

Pollen abundance and composition differed between vegetation types. SUMM was dominated by *Descurainia* (13–88%) and Fabaceae (2–45%) pollen, with the contribution of *Pinus* (1–32%) also considerable in some plots. Within PINE sites, *Pinus* (20–93%) was predominant, apart from in the highest PINE plot, while *Morella* (0–29%) and Ericaceae (0–10%) were also important contributors in the windward sites. Among shrub types, Fabaceae were well represented (2–19%), together with a high percentage of *Descurainia* (63%) in the highest PINE plot. LAUR samples were characterized by high values of Ericaceae (13–83%) and *Morella* (10–69%). Other notable trees were *Prunus* (0–8%), *Pinus* (0–5%), *Ilex* (0–4%), *Juniperus* (0–4%) and *Rhamnus* (0–3%), mainly represented in windward areas, whereas fern spores were relatively abundant in leeward plots (0–14%). Most notably, Lauraceae were poorly represented (<1.5%). THER sites featured generally low levels of tree pollen from both LAUR and PINE zones (e.g. Ericaceae 1–14%, *Morella* 1–26% and *Pinus* 0–5%), but also prominent contributions from taxa characteristic of the zone, including *Juniperus* (1–25%), *Pistacia* (0–35%), *Phoenix* (0–13%), *Visnea* (0–10%) and *Salix* (0–24%). Many shrubby and herbaceous taxa displayed higher percentages in THER: *Artemisia* (3–33%), *Rumex* (2–22%), *Cistus* (0–16%), Apiaceae (0–16%), *Jasminum* (0–13%), Asteraceae (0–12%), Poaceae (0–12%) and Urticaceae (0–10%). In COAS most common pollen types were shrubs and/or herbaceous taxa, including Poaceae (4–70%), *Euphorbia* (4–22%), Chenopodiaceae (3–20%), *Schizogyne* (2–46%) and Caryophyllaceae (0–9%). Some pollen types appeared well represented (>3%) in all vegetation types. They include Apiaceae, Asteraceae, Brassicaceae, Fabaceae, Liliaceae, Plantago, Poaceae, Pteridophyta, *Rumex* and Urticaceae. Although some pollen types from exotic plants have been recorded in THER, LAUR and PINE (e.g. *Cardiospermum*, Cupressaceae, *Eucalyptus*, *Quercus*, *Prunus*

dulcis and *Vitis*) none of them accounted for more than 1.5% and all have potential source plants within the local vegetation, if not always within the actual vegetation plots (see Table S.1, Supplementary data). Extra-regional types (taxa without possible source plants in the Canary Islands originated from plants growing in nearby continental regions) were not detected in our traps.

3.2. Pollen–vegetation relationships

In the ordination analysis, major vegetation types were shown to be clearly distinguished by their pollen rain spectra, except for some plots in PINE and SUMM, which overlapped (Fig. 3). Taxa contributing to the differences among vegetation types coincided with the dominant types shown in the pollen diagram (Figs. 2 and 3). Site positions on axis I of the DCA plot (Fig. 3) followed the elevational gradient of the island, while axis II identified a secondary gradient within THER samples. The length of axis I was over 5 SD units, indicating complete turnover in pollen composition between the highest and the lowest plots over the elevational gradient. In addition, pollen composition differed significantly among all vegetation types ($p < 0.01$) (Table 2). SIMPER showed a high dissimilarity between LAUR–SUMM (95.7), LAUR–COAS (96.7) and SUMM–COAS (96.3) (Table 2).

When vegetation data (plant cover percentage and basal area) were included in a second DCA, there was found to be a strong correspondence between pollen samples and the vegetation data for each vegetation type (Fig. 4), although the elevational zonation was no longer expressed on the first axis, requiring two dimensions to become evident (cf. Fig. 3). The first axis returns a strong gradient from open coastal habitats to closed cloud forest, with the second axis separating as extremes THER and SUMM zones. In LAUR plots, the dominance of AP was evident since total pollen composition matched better with basal area of trees than with cover of ferns, shrubs and herbaceous plants in the understory. Samples based on vegetation data were generally better separated than pollen samples probably due to higher species richness and taxonomic resolution, in the case of those plant species that do not belong to one of the pollen taxa recorded within the study.

Pollen–vegetation relationships were analysed independently for each vegetation type (Fig. 5). Significant differences between pollen and vegetation composition were detected in all vegetation types ($p < 0.01$) (Table 2), except for THER, for which variability among plots overrides any possible differences. Average dissimilarities between pollen and vegetation composition were comparable in SUMM (65.7), COAS (62.9), LAUR (59.1) and PINE (54.5) (Table 2).

Estimation of over- and under-represented pollen types was based on abundance data (see Materials and Methods). When the average abundance of a taxon was higher in the pollen signal we assumed over-representation (O) in this vegetation type, whereas higher abundance in plant cover or basal area indicated under-represented pollen types (U). Key taxa driving significant differences between pollen and vegetation were: *Descurainia* (O), *Pinus* (O), *Pterocarpus* (U), and Fabaceae (U) in SUMM; *Pinus* (O), *Morella* (O), *Descurainia* (O), Urticaceae (O), Ericaceae (O) and Fabaceae (U) in PINE; Ericaceae (O), *Morella* (O), Lauraceae (U), *Hedera* (U) and *Prunus* (U) in LAUR; and Poaceae (O), Chenopodiaceae (O), *Schizogyne* (O) and *Euphorbia* (U) in COAS; (Fig. 5; Table S.2, Supplementary data).

3.3. Fidelity and dispersibility

The representation of major taxa in the pollen rain based on the data for all sites was defined according to values of fidelity and dispersibility indices (Fig. 6). The following patterns were distinguished: 1) taxa having very high values of fidelity and dispersibility (over 80%), include only *Rumex*, Urticaceae and Poaceae; 2) taxa presenting high values of fidelity (70–100%) and moderate dispersibility (50–80%), include tree taxa, *Pinus*, Ericaceae, *Morella* and *Juniperus*, together with certain shrubs, herbs and ferns (*Artemisia*, Chenopodiaceae, Liliaceae and Pteridophyta); 3) taxa

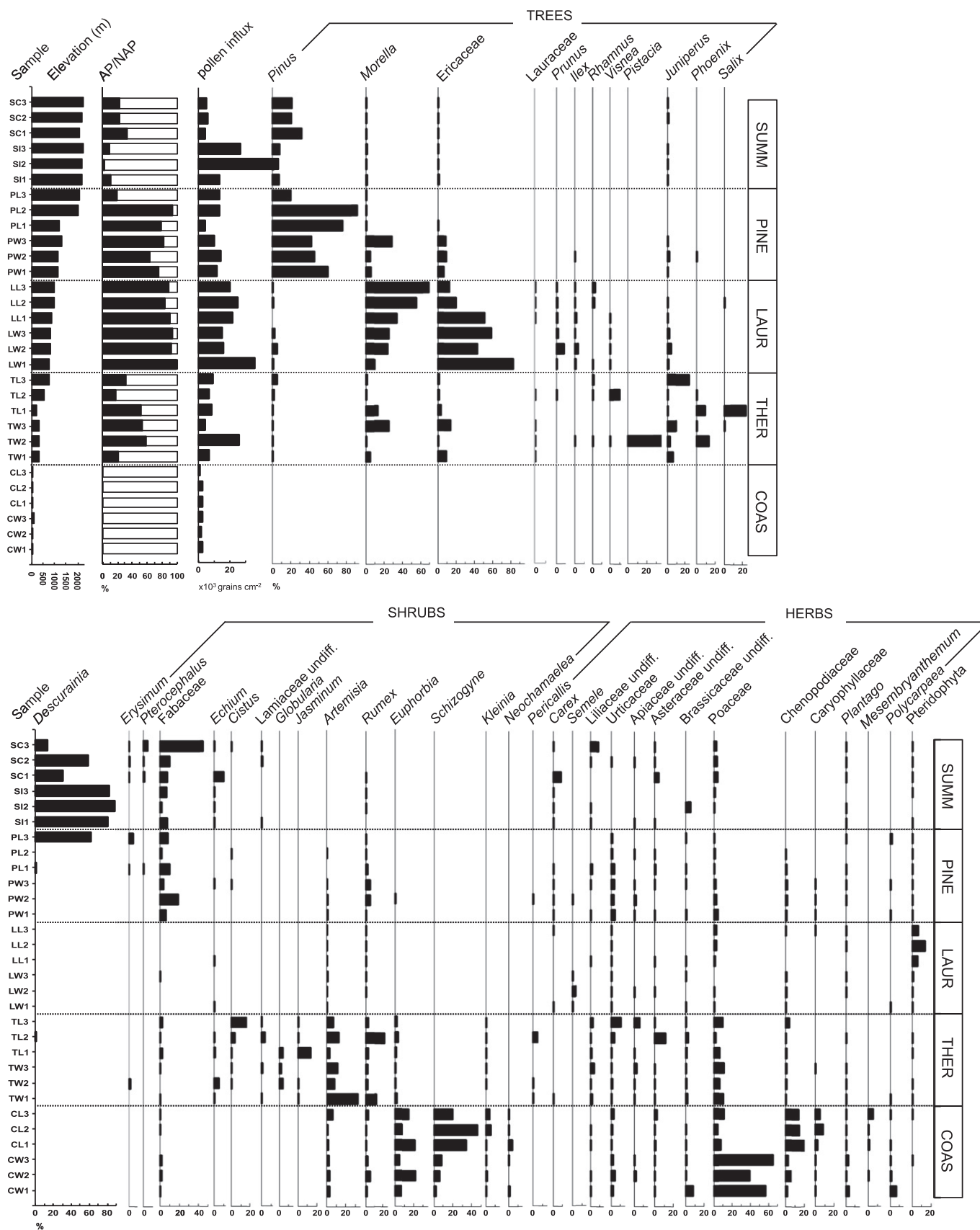


Fig. 2. Percentage diagram of arboreal (AP) and non-arboreal (NAP) modern pollen, collected on Tenerife for the period April 2010–July 2011, arranged by altitude and aspect. Selected taxa grouped in trees, shrubs and herbs are shown. AP/NAP ratio and pollen influx (grain cm⁻² year⁻¹) are shown in the first part of the diagram.

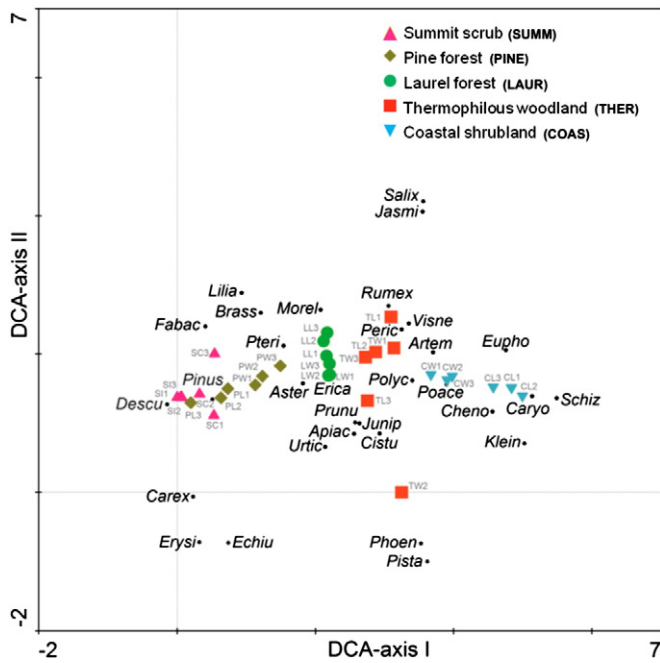


Fig. 3. DCA biplot based on pollen composition (%) across vegetation types on Tenerife for the period April 2010–July 2011 (total inertia = 5.1; cumulative variance = 23.8%). Only those taxa $\geq 5\%$ of abundance in at least one sample are shown. Taxa are labelled with the five initial letters of the family or genus (see Table S.1, Supplementary data). Name of plots indicate vegetation type (first letter), aspect (second letter) and elevational position (1–3 from lowest to highest elevation).

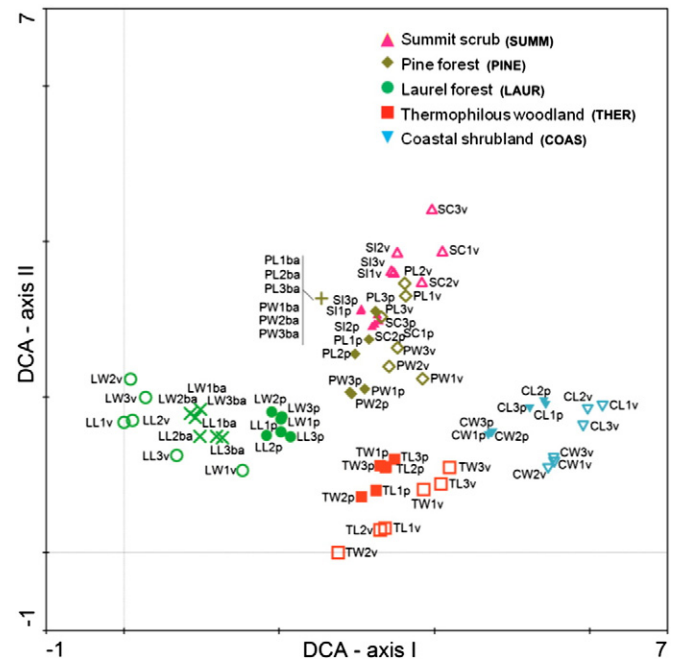


Fig. 4. DCA scatter-plot based on pollen composition (%) represented as filled symbols, plant cover (%) represented as open symbols, and basal area (m²/ha) represented as x-marks for LAUR and crosses for PINE, across vegetation types on Tenerife for the period April 2010–July 2011 (total inertia = 6.0; cumulative variance = 20.0%). Name of plots indicate vegetation type (first letter), aspect (second letter), elevational position (1–3 from lowest to highest elevation) and type of data (p = pollen, v = plant cover, ba = basal area).

characterized by fidelity values over 60%, but low dispersibility (less than 40%), comprising many tree taxa (*Heberdenia*, *Ilex*, *Phoenix*, *Prunus*, *Visnea*), and shrubs (*Convolvulus*, *Descurainia*, *Erysimum*, *Euphorbia*, *Fabaceae*, *Globularia*, *Jasminum*, *Justicia*, *Lycium*, *Neochamaelea*, *Rubia*,

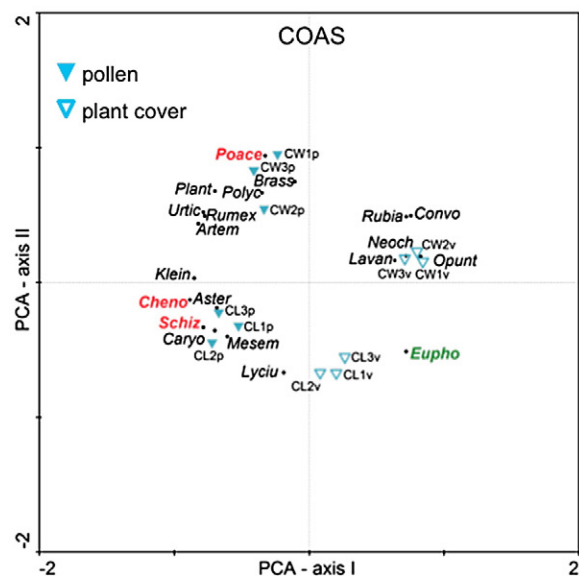
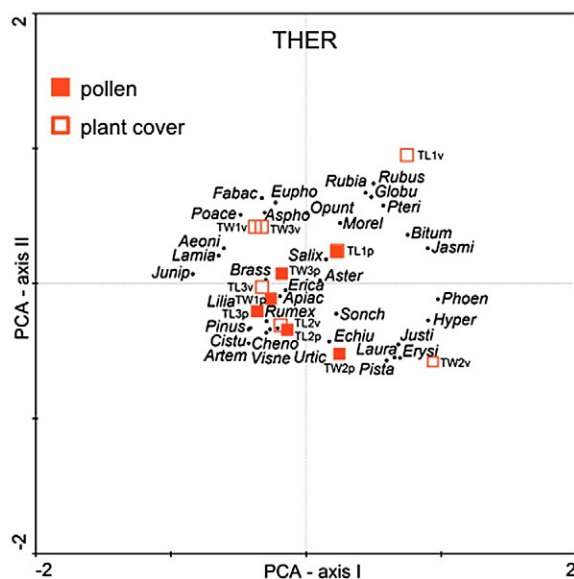
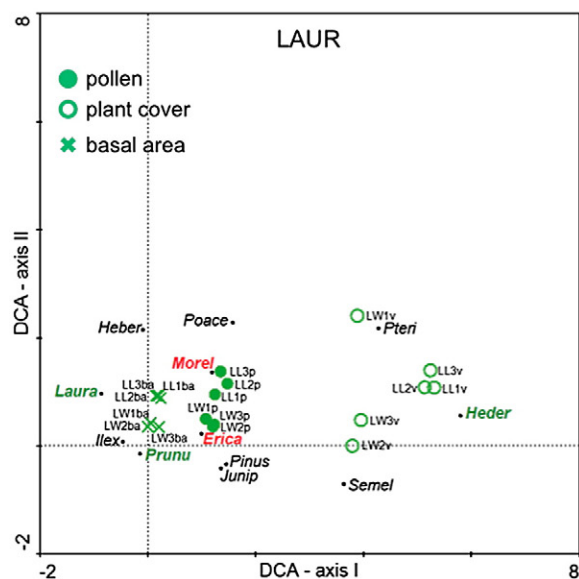
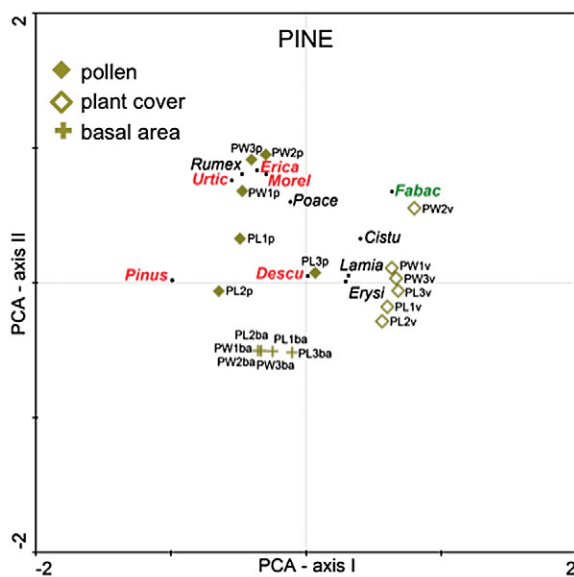
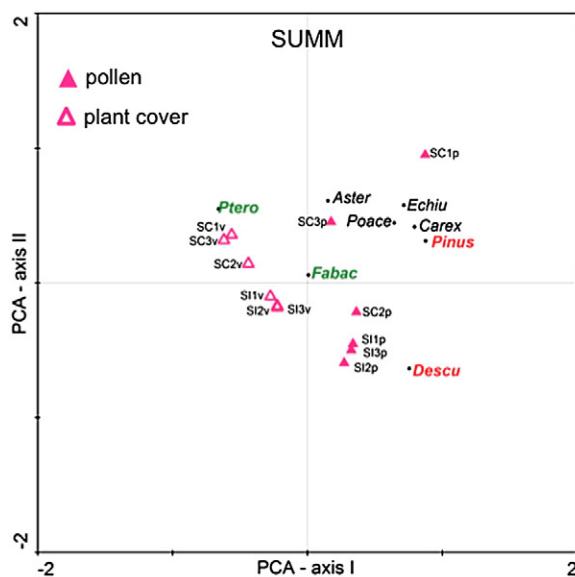
Rubus, *Schizogyne*) among others; 4) taxa defined by moderate to low fidelity (25–60%) and low dispersibility (less than 25%), including Lauraceae and *Pistacia* trees, several shrubs or herbs (*Asphodelus*, *Bituminaria*, *Cistus*, *Hedera*, *Pterocephalus*, *Periploca*); and finally

Table 2

Results of permutational-repeated measures analysis (ANOVA) and pair-wise t-test for comparisons of pollen, pollen-vegetation and modern-fossil pollen composition among vegetation types on Tenerife.^a

Pollen (%)			Pollen-vegetation (%)			Modern-fossil pollen (%)		
PERMANOVA	Pseudo-F	p(perm)	PERMANOVA	Pseudo-F	p(perm)	PERMANOVA	Pseudo-F	p(perm)
Vegetation types (n = 30)	10.825	0.000	Vegetation types (n = 60)	5.065	0.000	Forest types/pollen zones (n = 83)	29.303	0.000
			COAS (n = 12)	6.756	0.002			
			THER (n = 12)	2.586	0.011			
			LAUR (n = 12)	9.686	0.003			
			PINE (n = 12)	6.093	0.003			
			SUMM (n = 12)	7.724	0.003			
Pair-wise test Groups	t	p(MC)	Av. diss.			Pair-wise test Groups	t	p(MC)
COAS–THER	2.385	0.001	81.69			G1–THER	3.856	0.000
COAS–LAUR	4.158	0.000	96.72			G1–LAUR	4.799	0.000
COAS–PINE	3.580	0.000	91.52			G1–PINE	4.900	0.000
COAS–SUMM	3.738	0.000	96.27			G2–THER	5.244	0.000
THER–LAUR	2.799	0.001	81.95			G2–LAUR	4.438	0.000
THER–PINE	2.723	0.001	84.79			G2–PINE	6.810	0.000
THER–SUMM	3.026	0.000	92.42			L1–THER	5.873	0.000
LAUR–PINE	3.827	0.000	85.32			L1–LAUR	6.720	0.000
LAUR–SUMM	4.256	0.000	95.74			L1–PINE	6.746	0.000
SUMM–PINE	2.652	0.005	70.50			L2–THER	4.249	0.000
						L2–LAUR	5.112	0.000
						L2–PINE	5.178	0.000
						L3–THER	4.458	0.000
						L3–LAUR	5.234	0.000
						L3–PINE	5.915	0.000
								Av. sim.
								34.37
								31.26
								25.80
								35.15
								48.77
								25.19
								28.63
								34.66
								26.26
								29.35
								34.47
								23.95
								35.15
								38.81
								25.01

^a Bold values indicate significant differences ($p < 0.01$). Abbreviations stand for: vegetation type (COAS = coastal shrubland, THER = thermophilous woodland, LAUR = laurel forest, PINE = pine forest, SUMM = summit scrub) and pollen zones in Laguna Grande (G1 = 9600–5500 cal. yr BP, G2 = 5500–present cal. yr BP) and La Laguna (L1 = 4700–2900 cal. yr BP, L2 = 2900–2000 cal. yr BP, L3 = 2000–400 cal. yr BP). Av. diss.: average dissimilarity between groups, Av. sim.: average similarity between groups.



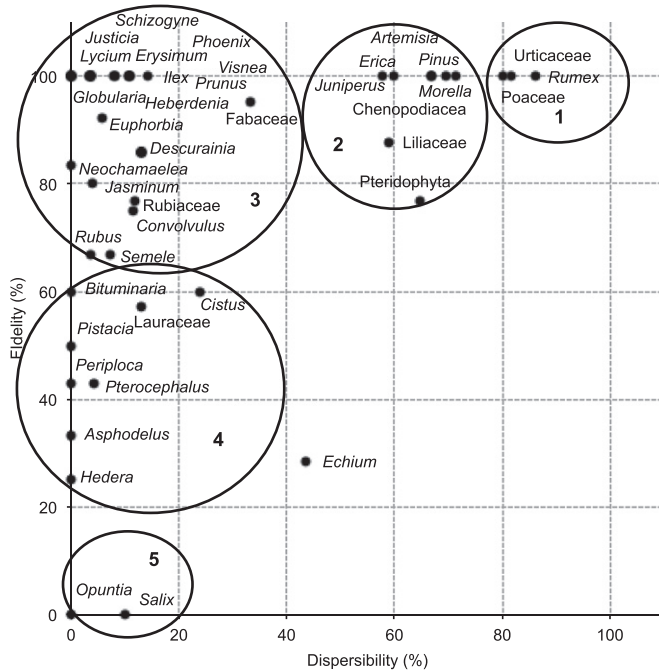


Fig. 6. Dispersibility index (percentage of sites where a taxon is only recorded in the pollen rain) versus fidelity index (percentage of sites where a taxon coincides both in pollen and vegetation) scores for individual taxa over 5% of abundance in at least one sample on Tenerife for the period April 2010–July 2011. Five patterns were recognised: 1) very high fidelity and dispersibility, 2) high fidelity and moderate dispersibility, 3) high fidelity and low dispersibility, 4) moderate to low fidelity and low dispersibility, and 5) very low fidelity and dispersibility.

5) taxa which showed very low values of both indices (0–10%), involve taxa absent in the pollen rain but present in the vegetation sampled (*Opuntia*), or which are present in the pollen rain but absent from the vegetation (*Salix*).

3.4. Fossil and modern pollen rain comparison

For the purpose of comparison of modern pollen rain samples with the fossil samples from the La Laguna (Tenerife) and Laguna Grande (La Gomera) sequences (de Nascimento et al., 2009; Nogué et al., 2013), the open habitat SUMM and COAS data were excluded to improve the ordination diagram's resolution, on the grounds that both fossil sequences recorded predominantly forest taxa throughout, as both were sampled from forest areas. The pollen composition differed significantly between the modern and fossil samples ($p < 0.01$) (Table 2). In an initial DCA analysis (Figure S.1, Supplementary data), the fossil sites were all clustered together at one end of axis I, with modern samples arranged by their similarities with fossil samples. As the modern samples from PINE were thus shown to be highly dissimilar from the fossil samples, the analysis was re-run selecting a PCA of modern THER and LAUR samples together with the fossil samples (Fig. 7). This resulted in a gradient from the youngest to the oldest fossil samples for both cores on axis I, in which the oldest fossil samples from La Laguna (L2 = 2900–2000 cal. yr BP) and L1 = 4700–2900 cal. yr BP) are the most dissimilar, with a trend over time through the more recent fossil samples (L3 = 2000–400 cal. yr BP)

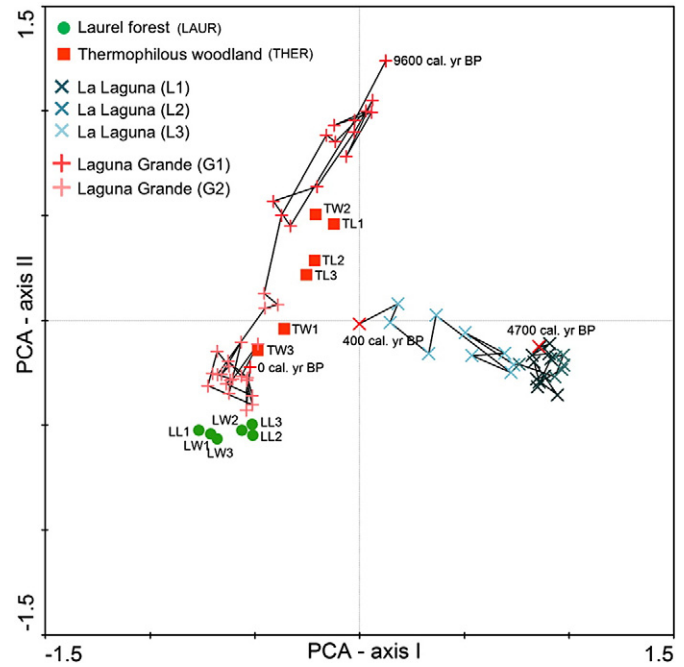


Fig. 7. PCA scatter-plot based on pollen composition (%) of modern samples from different forest types on Tenerife for the period April 2010–July 2011, and old sediments of La Laguna (Tenerife) = L, and Laguna Grande (La Gomera) = G (total variance = 1.0, cumulative variance = 56.5%). Different levels from both cores were classified according to pollen zones: L1 = 4700–2900 cal. yr BP, L2 = 2900–2000 cal. yr BP, L3 = 2000–400 cal. yr BP and G1 = 9600–5500 cal. yr BP, G2 = 5500–present cal. yr BP. Name of present pollen plots indicate vegetation type (first letter), aspect (second letter) and elevational position (1–3 from lowest to highest elevation). From the modern pollen sampling, only THER (T) and LAUR (L) forest samples were included: for an equivalent DCA analysis including PINE samples, see Figure S.1, Supplementary data.

towards modern THER and LAUR samples. This was confirmed from average similarities based on Bray–Curtis distance matrix, with the highest values obtained between L1–LAUR (34.6), L2–LAUR (34.5) and L3–LAUR (38.8) (Table 2). Axis II represented Laguna Grande fossil samples arranged by age, so that the oldest (G1 = 9600–5500 cal. yr BP) were closest in affinity to THER while the more recent fossil samples (G2 = 5500–present cal. yr BP) were intermediate between THER and LAUR in composition (Fig. 7). Best matches based on average similarities occurred between G1–THER (34.4) and G2–LAUR (48.8) (Table 2).

4. Discussion

4.1. Representation of Canarian vegetation by pollen

As found in other studies, there is a clear distinction between forests and open ecosystems in the AP/NAP ratio of the modern pollen rain (Fig. 2) (Davies and Fall, 2001; Cañellas-Boltà et al., 2009; Fall, 2012; Jantz et al., 2013). However, upwards transport of pollen from the forest zones and especially from the PINE zone, is evident in the sites located in the SUMM zone. This may reflect both exchange between zones and differences in pollen production (Pocknall, 1982; Kennedy et al., 2005; Collins and Bush, 2010). The higher leeward (drier) sites from the PINE zone also show a transitional nature in pollen rain and plant composition, with *Descurainia* (Brassicaceae) pollen exceeding

Fig. 5. PCA and DCA biplots based on pollen composition (%), plant cover (%) and basal area (m^2/ha) for each vegetation type on Tenerife for the period April 2010–July 2011 (SUMM: total variance = 1.0; cumulative variance = 74.7%, PINE: total variance = 1.0; cumulative variance = 70.7%, LAUR: total inertia = 2.3; cumulative variance = 40.1%, THER: total variance = 1.0; cumulative variance = 50.3%, COAS: total variance = 1.0; cumulative variance = 76.6%). As detected by SIMPER taxa contributing to dissimilarities between pollen and plant composition appear in red (taxa over-represented in pollen) and green (taxa under-represented in pollen). Only those taxa $\geq 5\%$ of abundance in at least one sample are shown. Taxa are labelled with the five initial letters of the family or genus (see Table S.1, Supplementary data). Name of plots indicate vegetation type (first letter), aspect (second letter), elevational position (1–3 from lowest to highest elevation) and type of data (p = pollen, v = plant cover, ba = basal area).

contributions from *Pinus* in one site (Figs. 1–3). The composition at these sites reflects the species-poor, sparsely vegetated character of contemporary treelines on Tenerife, especially in drier locations (del Arco et al., 2006) and these results show that determination of the uppermost treeline from pollen data may be inaccurate. An alternative approach that might be attempted in the future to detect past treeline positions is the use of phytoliths and stomata as indicators of the local occurrence of tree species, although this depends on finding suitable depositional environments in the right elevational locations. As found elsewhere (Markgraf, 1980), pollen transportation from upper forested elevations into the open coastal lowlands appears to be minimal, with AP lacking from the samples.

Our analyses demonstrate that there are distinctive pollen signals for each major vegetation type on Tenerife and that there is concordance between the modern pollen assemblages and vegetation composition of the sites surrounding the pollen traps (Figs. 3 and 4). In the only previous modern pollen study on a Macaronesian island, similar results were obtained for the local vegetation of Flores (Connor et al., 2013).

4.2. Pollen–vegetation relationships at the community level

Within vegetation types we detected significant differences between pollen and plant representation, with some taxa identified as over- or under-represented in the pollen rain (Fig. 5). Pollen production varies among species depending on biological and ecological parameters such as pollination system, plant life forms, flower traits, vegetation dynamics and structure, or climate (Faegri and Iversen, 1989). Over-representation occurs because pollen is produced abundantly or disperses easily (Faegri and Iversen, 1989). Hence, for example, wind-pollinated plants typically are better represented in pollen rain than are insect- or self-pollinated species.

Many characteristic species of Canarian plant communities were under-represented in our pollen data (Fig. 5), most probably because they all belong to entomophilous families (Eriksson and Bremer, 1992; Franchi and Pacini, 1996). Examples include *Adenocarpus viscosus* and *Spartocytisus supranubius* (included in the Fabaceae type), and *Pteroccephalus lasiospermus*, insect-pollinated species of the SUMM zone (Dupont et al., 2003); the insect and self-pollinated shrub *Chamaecytisus proliferus* (Webb and Shand, 1985) and *Adenocarpus* spp. (also Fabaceae type) in the PINE zone; and *Laurus novocanariensis*, *Prunus lusitanica* and *Hedera helix* in the LAUR zone. There is evidence of bee and fly-pollination of *L. novocanariensis* (Forfang and Olesen, 1998). In addition, Lauraceae pollen grains have a very thin exine and are often badly preserved or are corroded during pollen extraction procedures (Van der Merwe et al., 1990; Connor et al., 2013). In this work, despite reducing acetolysis treatment to just two minutes, Lauraceae pollen was always below 2% in all samples. Insect-pollination has been detected in *Prunus* species (Gutián et al., 1993) although pollen under-representation for this taxon may be also attributable to its mast flowering, leading to lower pollen production in certain years (Gerasimidis et al., 2006; Pías and Gutián, 2006). Under-representation of *Euphorbia balsamifera*, *E. canariensis* and *E. lamarckii* in the COAS sites is consistent with other modern pollen studies from arid regions, which list *Euphorbia* as typically entomophilous (Carrión, 2002; Amami et al., 2010).

Several over-represented taxa could be identified at the community level (Fig. 5), mostly comprising wind-pollinated plants, but in cases combining wind and insect-pollination strategies (Eriksson and Bremer, 1992; Franchi and Pacini, 1996). For example, *Descurainia bourgeauna* is among the most widespread species in the SUMM zone, and although it is a member of a typically entomophilous family (Brassicaceae) participating in the pollination network (Valido et al., 2011), it provided the highest pollen influx in the SUMM zone (Fig. 2). As discussed above, pine pollen is over-represented in SUMM sites, reflecting upslope transport from the PINE zone (although there are some scattered pines that may be local contributors). Other pine

species are outstanding pollen producers and their pollen disperses easily by wind (Stevenson, 1985; Carrión, 2002; Fall, 2012). Pine is indeed a classical example of an over-represented pollen type (Faegri and Iversen, 1989). Both *Descurainia bourgeauna* and *Pinus canariensis* are also over-represented in PINE sites, but whereas *P. canariensis* is the dominant tree on this vegetation type, *D. bourgeauna* is completely absent from these plots, pointing to some dispersal ability of its pollen, at least towards the PINE zones that are close to SUMM vegetation. Urticaceae was also over-represented in PINE zone samples despite its low pollen contribution (3%) and the absence of Urticaceae plants in PINE plots. Urticaceae is a frequent type of airborne pollen (Spieksma et al., 2003), usually originating from ruderal plants (e.g. *Forsskaolea angustifolia*) that are not common in well-preserved areas (see Table S.1, Supplementary data). Two other tree taxa, *Morella faya* and *Erica* spp., which are only present at the three windward PINE locations, provided pollen representation in all PINE sites. High pollen productivity is readily appreciable in the field for these two taxa when large quantities of pollen can be detected as they are blown from their branches. Long-distance pollen dispersal can be deduced from the occurrence of both pollen types at PINE leeward expositions, which are several kilometres away (at least 20 km) from the current distribution of both trees in the island (del Arco et al., 2006). Contributions of *Morella* and Ericaceae pollen types were also high in relation to the abundance of these trees in LAUR sites. Over-representation of *M. faya* pollen has also been recorded from patches of *L. azorica* on the island of Flores, but *Erica* pollen showed a good correspondence with its representation in surrounding vegetation in that study (Connor et al., 2013). Ericaceae species have been classified as being primarily entomophilous (Eriksson and Bremer, 1992; Carrión, 2002; Amami et al., 2010) but some *Erica* species also show bird- or wind-pollination syndromes (Rebello and Siegfried 1985), including both Canarian species. *E. scoparia* is considered anemophilous and produces large numbers of pollen grains per flower in the sclerophyllous shrublands of southwestern Spain (Herrera, 1987). *E. arborea* combines both wind- and insect-pollination modes (Franchi and Pacini, 1996). In addition, they are also considered to be bee foraging plants in the Canaries (La-Serna et al., 2002). In COAS samples, pollen from Poaceae, Chenopodiaceae and Schizogyne was over-represented compared to the relatively low cover (always below 6%) of their corresponding parent plants, represented mainly by *Hyparrhenia hirta*, *Cenchrus ciliaris* and *Aristida adscensionis* (all Poaceae), *Salsola divaricata* and *Patellifolia patellaris* (both Chenopodiaceae) and *Schizogyne sericea* (a shrubby Asteraceae). Asteraceae, Chenopodiaceae and Poaceae are largely wind-pollinated families (Eriksson and Bremer, 1992; Franchi and Pacini, 1996) and are usually dominant types in coastal areas of the Mediterranean (Carrión, 2002; Fall, 2012). The high variability found in THER, where patches of vegetation are dominated by different tree species, precludes detailed examination of over- and under-representation for this zone (Fig. 5).

4.3. Indicator taxa

When considering co-occurrence of pollen and plant taxa regardless of the vegetation type, indices of fidelity and dispersibility help to decide whether a taxon can be a good indicator of its nearby presence or whether its pollen is effectively dispersed from its source. We found that pollen of *Rumex*, Urticaceae and Poaceae is well dispersed (Group 1 in Fig. 6). In fact, their pollen types appear in almost all plots (Fig. 2) such that they lack a diagnostic value if only presence/absence data are considered. In the case of *Rumex*, it did not qualify as over-represented in any vegetation type, suggesting a strong dispersal ability rather than high productivity for this pollen type. There are quite a few taxa considered moderately dispersed that show a high correlation between pollen and source plants (Group 2 in Fig. 6). Among these well-represented types are trees like *Pinus*, *Erica* spp., *Juniperus* and *Morella*. *Erica* and *Juniperus* were also well represented in modern pollen on the island of Flores (Connor et al., 2013). However, pollen

from these trees can also be easily dispersed to neighbouring vegetation types, as shown by their over-representation in adjacent zones (SUMM, PINE and LAUR, see Fig. 5). Therefore the adoption of specific threshold percentage values may be necessary to ascertain their local or regional presence. Several LAUR trees (*Heberdenia*, *Ilex*, *Prunus*, *Visnea*), and many taxa from THER (*Convolvulus*, *Globularia*, *Jasminum*, *Justicia*, *Phoenix*, *Rubia*, *Rubus*) with low dispersibility but relatively high fidelity values (Group 3 in Fig. 6) would appear to be good indicators of local occurrence when the pollen is found. Within this group are also some over- and under-represented pollen types from SUMM/PINE (*Descurainia*, Fabaceae) and COAS (*Euphorbia*), which can thus also be used to confirm their local presence notwithstanding that their abundance may be over- or under-represented. Group 4, showing little contribution to pollen rain and poor transport ability, includes some important floristic elements of Canarian ecosystems, *Pterocephalus* in SUMM, *Cistus* in PINE, Lauraceae in LAUR, *Pistacia* in THER and *Periploca* in COAS sites (Fig. 6). Therefore, the lack of these types from pollen assemblages cannot be interpreted as absence in the local vegetation. Finally, we have two rare exceptions, the exotic *Opuntia*, an insect-pollinated plant, which is totally missing in the pollen rain, but with considerable presence (5% plant cover) in THER and COAS, and *Salix canariensis*, which was recorded in pollen rain but not in vegetation (Group 5, Fig. 6). In this case pollen came from outside the plot where several *Salix* trees grow.

Despite the existence of good indicator taxa in all vegetation types, floristically important taxa of SUMM (Fabaceae shrubs), LAUR (Lauraceae trees) and COAS (*Euphorbia* shrubs) zones are under-represented according to both presence and abundance data. This situation therefore requires the use of indicative groups of taxa and their occurrence in certain proportions in order to differentiate vegetation types from pollen assemblages. Over-representation of other trees (Ericaceae, *Morella*, *Pinus*), shrubs and herbs (Chenopodiaceae, *Descurainia*, Poaceae, *Rumex*, Urticaceae) that are also very common in the vegetation, suggests that these types should be interpreted with caution in the fossil record.

4.4. Extra-regional pollen

Pollen transport from continental areas can sometimes provide a significant signal within insular pollen rain (Dodson, 1976, 1982; McGlone and Meurk, 2000; Bottema and Sarpaki, 2003; Collins and Bush, 2010; van der Knaap et al., 2012), particularly in communities where local pollen production is low. In a recent study to monitor airborne pollen, Izquierdo et al. (2011) inferred extra-regional pollen transport to Tenerife for several taxa, *Artemisia*, *Casuarina*, Cyperaceae, Chenopodiaceae/Amaranthaceae, *Olea*, Poaceae, *Quercus* and *Vitis* (all but *Casuarina* also found in our study; Table S.1, Supplementary data). In all cases potential source plants do grow wild on the island (Acebes et al., 2009), but Izquierdo et al. (2011) argued that outstanding peak events within the pollen signal represented evidence of their long-range transport. Specifically, *Olea*, *Quercus* and *Vitis* types were estimated as having the highest pollen proportions originated from extra-regional sources. However, we note that while a few of the listed taxa were classed as over-represented in our study, e.g. *Artemisia*, Chenopodiaceae and Poaceae (Figs. 5 and 6), others contribute only low proportions to the pollen rain, e.g. Cyperaceae, *Olea*, *Quercus* and *Vitis* (Table S.1, Supplementary data). Direct comparison between the two studies is complicated due to the different sampling method (suction traps), different time period (24 months) and increased time resolution (daily measurements), and also different spatial resolution (two stations and urban areas) of the study by Izquierdo et al. (2011). Furthermore, all the identified pollen types in our study that derive from non-native taxa, *Cardiospermum*, Cupressaceae, *Prunus dulcis*, *Quercus* and *Vitis* (Table S.1, Supplementary data), could have been sourced from naturalised plant species recorded on Tenerife. Hence, while we cannot rule out a long distance pollen contribution to the pollen rain recorded in our study, we are unable to distinguish an extra-regional (continental) component in these data. Additionally, the relatively high pollen

influx originated from local vegetation (Fig. 2), could make the amount of extra-regional pollen relatively insignificant in terms of the overall pollen rain signal (Faegri and Iversen, 1989).

4.5. Implications for fossil pollen records

The analysis of modern pollen rain presented here can be used to re-appraise the interpretation of Canarian fossil pollen diagrams (de Nascimento et al., 2009; Nogué et al., 2013). In practice, the correspondence found between modern pollen rain and the samples from the La Gomera core supports the hypothesis of a shift in forest composition in response to regional climate change (Nogué et al., 2013). First, fossil pollen assemblages in the oldest sector of the Laguna Grande core (La Gomera) (9600–5500 cal. yr BP) resemble THER pollen rain more closely than they do LAUR pollen rain (Fig. 7). There was, in particular, close similarity with the composition of the Barranco de El Cercado (TL1) site, which was sampled in order to obtain the pollen signal of Canarian palm and willow communities, characterised by *Phoenix canariensis* and *Salix canariensis*, respectively. As we have shown above, both trees are indeed well represented in the pollen rain in that site (Fig. 2). This result is consistent with the possible presence of both trees in the vicinity of the lagoon, as was previously deduced from the fossil pollen record. In addition, low values of *Erica* and *Morella* (always below 15%) within this period (see Nogué et al., 2013) point to a reduced or distant occurrence of the laurel forest. Within the most recent sector of this core (5500–present cal. yr BP) fossil pollen matches more closely with LAUR pollen composition or is intermediate between LAUR and THER sites (Fig. 7), mainly because of higher percentages of *Erica* and *Morella* (up to 50%), and the minor contribution of other key taxa that are good indicators of this forest, including Lauraceae, *Prunus* and *Ilex* (Fig. 6). Whether the Laguna Grande forest of this period corresponded to a fully developed laurel forest or to the *Morella-Erica* woody heath remains unclear since Lauraceae species are notably under-represented in modern pollen rain in LAUR sites (Figs. 2 and 5; Table S.1, Supplementary data) and we have no reference for the pollen signal of the *Morella-Erica* woody heath. Further field sampling to provide a still better characterisation of the pollen signal of the different formations of the monteverde would be of great value in the identification of these two forest types and the interpretation of fossil records from these islands.

On Tenerife, there is no close match between the older sectors of La Laguna core (4700–2000 cal. yr BP) and any of the modern pollen assemblages (Fig. 7). The dominance of *Carpinus* and *Quercus* in the pollen records for this period (de Nascimento et al., 2009) has no modern analogue in the vegetation of the island. Other accompanying pollen types found in that period, *Cistus*, *Ilex*, *Juniperus*, Lauraceae, *Prunus*, *Phoenix*, *Salix* or *Visnea*, represent a mixture of species that can be interpreted as the ecotone between laurel forest and thermophilous woodlands, presumed to be growing near the lake by that time. Values of fossil pollen for *Carpinus* (up to 25%) and *Quercus* (5–10%) obtained during this period indicate that both trees were important within the local vegetation, although it remains uncertain whether they were growing within the laurel forest and/or thermophilous woodland zones. In contrast to the fossil pollen values from La Laguna, *Carpinus* pollen has not been detected in any trap, while *Quercus* percentages, either coming from semi-natural populations currently growing on the island or from extra-regional sources (Izquierdo et al., 2011), were insignificant (less than 0.5%). In the most recent period (2000–400 cal. yr BP) fossil pollen composition becomes closer to contemporary LAUR pollen rain (Fig. 7) as values of *Morella* rise to 25%. This agrees with the interpretation that the former forest was replaced during this period by vegetation similar to the current laurel forest and that this happened following human colonization of the island (de Nascimento et al., 2009). Again, the under-representation of Lauraceae species hampers our ability to determine actual forest composition in detail. In addition, the already mentioned representative taxa from LAUR and THER were also present within this section of the fossil record, implying the proximity of both

vegetation types (or their intermingling in a no-modern analogue palaeo-forest) during the whole period.

Relatively low and constant values of *Pinus* pollen in both records (0–6% in Laguna Grande and 1–10% in La Laguna) corroborate the presence of pine forests at a regional scale (compare Figs. 2, 5, 6, Figure S.1, Supplementary data). Likewise, from the absence of characteristic taxa of SUMM and COAS in both palaeorecords, we can conclude that shrubland vegetation was not growing in close proximity to either of the coring sites.

5. Conclusions

Major vegetation types on Tenerife generate distinctive pollen signals and there is concordance between modern pollen assemblages and vegetation composition. Whereas many pollen types were not restricted to a single vegetation type, their contributions differ significantly between the different vegetation types, providing diagnostic value. However, we detected upwards transport of pollen, especially from the PINE forest zone to the SUMM open scrublands, so that the determination of the uppermost treeline from pollen data may be inaccurate. Within vegetation types we identified some important floristic elements to be over-represented (*Pinus*, *Morella* and Ericaceae trees, Chenopodiaceae, *Descurainia*, Poaceae, *Rumex* and Urticaceae herbs and shrubs) or under-represented (Lauraceae trees, Fabaceae and *Euphorbia* shrubs) in the pollen rain. In particular, the under-representation of Lauraceae species hampers our ability to distinguish between the laurel forest and the *Morella-Erica* woody heath. Thus we suggest that groups of taxa and thresholds values of pollen contribution should be considered when discriminating vegetation from pollen data. In addition several taxa from LAUR forest zones (*Heberdenia*, *Ilex*, *Prunus* and *Visnea*) and THER zones (*Convolvulus*, *Globularia*, *Jasminum*, *Justicia*, *Phoenix*, *Rubia* and *Rubus*) appear to be good indicators of local occurrence when pollen is found, as shown by their high fidelity values.

In our sampling sites we did not detect extra-regional pollen types due to both the difficulty of distinguishing between continental and native pollen types, and the relatively high pollen supply originating from local vegetation. While we do not discard the possibility of sporadic contributions from long-distance pollen sources, we find no evidence of such sources distorting the pollen signal from within the archipelago.

Our results are consistent with our previous descriptions and interpretations of past vegetation change from fossil pollen analysis on La Gomera and Tenerife (de Nascimento et al., 2009; Nogué et al., 2013). No modern analogue could be assigned to the vegetation occurring in La Laguna before human colonization of Tenerife, which appears to be the event that initiated the transition from the pre-historic no-analogue forest towards the current laurel forest types. On La Gomera, the vegetation nearby the former lake in Laguna Grande during the early Holocene resembled the Canarian palm and willow communities, but progressively changed in composition around 5500 cal. yr BP, to become more similar to the contemporary laurel forest.

Acknowledgements

This work was funded by the Spanish Ministry of Science and Innovation (project: CGL 2009–10939). Field work in Natural Protected Areas was made possible by permissions from the Área de Medio Ambiente (Cabildo Insular de Tenerife), and the Consejería de Medio Ambiente (Gobierno de Canarias) to work at El Teide National Park. We are also grateful to the owners of Finca de Viña Vieja who provided access to their property at Barranco de El Cercado. Finally, for their collaboration in the field work we thank José Ramón Arévalo, Carlos G. Escudero, Gustavo Morales, Celia García, Alexandra Rodríguez, Jorge Durán, Cristina Blandino, Katharina Eller and Alistair Domínguez.

Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.revpalbo.2014.11.002>.

References

- Acebes, J.R., León, M.C., Rodríguez, M.L., del Arco, M., García, A., Pérez, P.L., Rodríguez, O., Martín, V.E., Wildpret, W., 2009. Pteridophyta, Spermatophyta. In: Arechavaleta, M., Rodríguez, S., Zurita, N., García, A. (Eds.), *Lista De Especies Silvestres De Canarias. Hongos, Plantas y Animales Terrestres*. Gobierno de Canarias, pp. 218–220.
- Amami, B., Muller, S.D., Rhazi, L., Grillas, P., Rhazi, M., Bouahim, S., 2010. Modern pollen-vegetation relationships within a small Mediterranean temporary pool (western Morocco). *Rev. Palaeobot. Palynol.* 162, 213–225.
- Anderson, M., Gorley, R., Clarke, K., 2008. *Permanova + for primer: Guide to software and statistical methods*. Primer-E Ltd., Plymouth, UK.
- Behling, H., Cohen, M.C.L., Lara, R.J., 2001. Studies on Holocene mangrove ecosystem dynamics of the Bragança Peninsula in north-eastern Pará, Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 167, 225–242.
- Bennett, K.D., 2008. *Psimpoll 4.26*. Department of Earth Sciences, Uppsala University, Uppsala, Sweden.
- Bennett, K.D., Willis, K.J., 2001. Pollen. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Volume 3: Terrestrial, algal, and siliceous indicators*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 5–32.
- Birks, H.J.B., Birks, H.H., 1980. *Quaternary palaeoecology*. Arnold, London.
- Bottema, S., Sarpaki, A., 2003. Environmental change in Crete: a 9000-year record of Holocene vegetation history and the effect of the Santorini eruption. *The Holocene* 13, 733–749.
- Bradshaw, R.H.W., Webb, T., 1985. Relationship between contemporary pollen and vegetation data from Wisconsin and Michigan, USA. *Ecology* 66, 712–737.
- Cañellas-Boltà, N., Rull, V., Vigo, J., Mercadé, A., 2009. Modern pollen-vegetation relationships along an altitudinal transect in the central Pyrenees (southwestern Europe). *The Holocene* 19, 1185–1200.
- Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. *J. For.* 39, 388–394.
- Carrión, J.S., 2002. A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. *Rev. Palaeobot. Palynol.* 120, 217–232.
- Collins, A., Bush, M.B., 2010. An analysis of modern pollen representation and climatic conditions on the Galápagos Islands. *The Holocene* 21, 237–250.
- Connor, S.E., van der Knaap, W.O., van Leeuwen, J.F.N., Kuneš, P., 2013. Holocene palaeoclimate and palaeovegetation on the islands of Flores and Pico. In: Fernández-Palacios, J.M., de Nascimento, L., Hernández, J.C., Clemente, S., González, A., Díaz-González, J.P. (Eds.), *Climate change perspectives from the Atlantic: Past, present and future*. Servicio de Publicaciones Universidad de La Laguna, La Laguna.
- Davies, M.B., 1963. On the theory of pollen analyses. *Am. J. Sci.* 261, 897–912.
- Davies, C.P., Fall, P.L., 2001. Modern pollen precipitation from an elevational transect in central Jordan and its relationship to vegetation. *J. Biogeogr.* 28, 1195–1210.
- Davis, O.K., 1984. Pollen frequencies reflect vegetation patterns in a Great Basin (U.S.A.) mountain range. *Rev. Palaeobot. Palynol.* 40, 295–315.
- de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C., Whittaker, R.J., 2009. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *J. Biogeogr.* 36, 499–514.
- del Arco, M.J., Wildpret, W., Pérez de Paz, P.L., Rodríguez, O., Acebes, J.R., García, A., Martín, V.E., Reyes, J.A., Salas, M., Díaz, M.A., Bermejo, J.A., González, R., Cabrera, M.V., García, S., 2006. *Mapa de Vegetación de Canarias. GRAFCAN*, Santa Cruz de Tenerife.
- del Arco, M.J., González-González, R., Garzón-Machado, V., Pizarro-Hernández, B., 2010. Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity Conserv.* 19, 3089–3140.
- Deng, Y., Horrocks, M., Ogden, J., Anderson, S., 2006. Modern pollen-vegetation relationships along transects on the Whangapoua Estuary, Great Barrier Island, northern New Zealand. *J. Biogeogr.* 33, 592–608.
- Dodson, J.R., 1976. Modern pollen spectra from Chatham Island, New Zealand. *N. Z. J. Bot.* 14, 341–347.
- Dodson, J.R., 1982. Modern pollen rain and recent vegetation history on Lord Howe Island evidence of human impact. *Rev. Palaeobot. Palynol.* 38, 1–21.
- Dupont, Y.L., Hansen, D.M., Olesen, J.M., 2003. Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* 26, 301–310.
- Eriksson, O., Bremer, B., 1992. Pollination systems, dispersal modes, life forms, and diversification rates in angiosperm families. *Evolution* 46, 258–266.
- Faegri, K., Iversen, J., 1989. *Textbook of pollen analysis*. 4th ed. Blackburn Press, New Jersey.
- Fagerlin, K., 1952. The real significance of pollen diagrams. *Bot. Notiser* 105, 185–224.
- Fall, P., 2012. Modern vegetation, pollen and climate relationships on the Mediterranean island of Cyprus. *Rev. Palaeobot. Palynol.* 185, 79–92.
- Fernández-Palacios, J.M., de Nicolás, J.P., 1995. Altitudinal patterns of vegetation variation on Tenerife. *J. Veg. Sci.* 6, 183–190.
- Fernández-Palacios, J.M., Otto, R., Delgado, J.D., Arévalo, J.R., Naranjo, A., González, F., Morici, C., Barone, R., 2008. *Los Bosques Termófilos de Canarias. Proyecto LIFE04/NAT/ES/000064, Cabildo Insular de Tenerife*, Santa Cruz de Tenerife.
- Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *J. Biogeogr.* 38, 226–246.

- Fletcher, M.-S., Thomas, I., 2007a. Holocene vegetation and climate change from near Lake Pedder, south-west Tasmania, Australia. *J. Biogeogr.* 34, 665–677.
- Fletcher, M.-S., Thomas, I., 2007b. Modern pollen–vegetation relationships in western Tasmania, Australia. *Rev. Palaeobot. Palynol.* 146, 146–168.
- Forfang, A.-S., Olesen, J.M., 1998. Male-biased sex ratio and promiscuous pollination in the dioecious island tree *Laurus azorica* (Lauraceae). *Plant Syst. Evol.* 212, 143–157.
- Franchi, G.G., Pacini, E., 1996. Types of pollination and seed dispersal in Mediterranean plants. *G. Bot. Ital.* 130, 579–585.
- Gajewski, K., 1995. Modern and Holocene pollen assemblages from some small Arctic lakes on Somerset Island, NWT, Canada. *Quat. Res.* 44, 228–236.
- Gerasimidis, A., Panajiotidis, S., Hicks, S., Athanasiadis, N., 2006. An eight-year record of pollen deposition in the Pieria mountains (N. Greece) and its significance for interpreting fossil pollen assemblages. *Rev. Palaeobot. Palynol.* 141, 231–243.
- Gutián, J., Gutián, P., Sánchez, J.M., 1993. Reproductive biology of two *Prunus* species (Rosaceae) in the Northwest Iberian Peninsula. *Plant Syst. Evol.* 185, 153–165.
- Herrera, J., 1987. Flower and fruit biology in southern Spanish Mediterranean shrublands. *Ann. Mo. Bot. Gard.* 74, 69–78.
- Izquierdo, R., Belmonte, J., Avila, A., Alarcón, M., Cuevas, E., Alonso-Pérez, S., 2011. Source areas and long-range transport of pollen from continental land to Tenerife (Canary Islands). *Int. J. Biometeorol.* 55, 67–85.
- Jackson, S.T., Dunwiddie, P.W., 1992. Pollen dispersal and representation on an offshore island. *New Phytol.* 122, 187–202.
- Jacobson, G.L., Bradshaw, R.H.W., 1981. The selection of sites for paleovegetational studies. *Quat. Res.* 16, 80–96.
- Jantz, N., Homeier, J., León-Yáñez, S., Moscoso, A., Behling, H., 2013. Trapping pollen in the tropics – Comparing modern pollen rain spectra of different pollen traps and surface samples across Andean vegetation zones. *Rev. Palaeobot. Palynol.* 193, 57–69.
- Kennedy, L.M., Horn, S.P., Orvis, K.H., 2005. Modern pollen spectra from the highlands of the Cordillera Central, Dominican Republic. *Rev. Palaeobot. Palynol.* 137, 51–68.
- Klaus, W., 1989. Mediterranean pines and their history. *Plant Syst. Evol.* 162, 133–163.
- La-Serna, I.E., Méndez, B., Gómez, C., 2002. Pollen spectra of different unifloral honeys from La Palma (Canary Islands, Spain). *Grana* 41, 48–57.
- Lepš, J., Šmilauer, P., 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, UK.
- Lozhkin, A.V., Anderson, P.M., Varatanyan, S.L., Brown, T.A., Belaya, B.V., Kotov, A.N., 2001. Late Quaternary paleoenvironments and modern pollen data from Wrangel Island (Northern Chukotka). *Quat. Sci. Rev.* 20, 217–233.
- Markgraf, V., 1980. Pollen dispersal in a mountain area. *Grana* 19, 127–146.
- McGlone, M.S., Meurk, C.D., 2000. Modern pollen rain, subantarctic Campbell Island, New Zealand. *N. Z. J. Ecol.* 24, 181–194.
- McGlone, M.S., Moar, N.T., 1997. Pollen–vegetation relationships on the subantarctic Auckland Islands, New Zealand. *Rev. Palaeobot. Palynol.* 96, 317–338.
- Niemann, H., Brunschön, C., Behling, H., 2010. Vegetation/modern pollen rain relationship along an altitudinal transect between 1920 and 3185 m a.s.l. in the Podocarpus National Park region, southeastern Ecuadorian Andes. *Rev. Palaeobot. Palynol.* 159, 69–80.
- Nogué, S., de Nascimento, L., Fernández-Palacios, J.M., Whittaker, R.J., Willis, K.J., 2013. The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. *J. Ecol.* 101, 368–377.
- Otto, R., Barone, R., Delgado, J.D., Arévalo, J.R., Garzón-Machado, V., Cabrera-Rodríguez, F., Fernández-Palacios, J.M., 2012. Diversity and distribution of the last remnants of endemic juniper woodlands on Tenerife, Canary Islands. *Biodiversity Distrib.* 21, 1811–1834.
- Pias, B., Gutián, P., 2006. Breeding system and pollen limitation in the masting tree *Sorbus aucuparia* L. (Rosaceae) in the NW Iberian Peninsula. *Acta Oecol.* 29, 97–103.
- Pocknall, D.T., 1982. Modern pollen spectra from mountain localities, South Island, New Zealand. *N. Z. J. Bot.* 20, 361–371.
- Prentice, I.C., 1985. Pollen representation, source area and basin size: toward a unified theory of pollen analysis. *Quat. Res.* 23, 76–86.
- Rebelo, A.G., Siegfried, W.R., 1985. Colour and size of flowers in relation to pollination of *Erica* species. *Oecologia* 65, 584–590.
- Reille, M., 1992. Pollen Et Spores D'Europe Et D'Afrique Du Nord. Laboratoire de Botanique historique et Palynologie, Marseille.
- Reille, M., 1995. Pollen et Spores D'Europe Et D'Afrique Du Nord Supplément 1. Laboratoire de Botanique historique et Palynologie, Marseille.
- Reille, M., 1998. Pollen Et Spores D'Europe Et D'Afrique Du Nord Supplément 2. Laboratoire de Botanique historique et Palynologie, Marseille.
- Salas, M.R., 1983. Long-distance pollen transport over the southern Tasman Sea: evidence from Macquarie Island. *N. Z. J. Bot.* 21, 285–292.
- Spiekma, F.Th.M., Corden, J.M., Detandt, M., Millington, W.M., Nikkels, H., Noland, N., Schoenmakers, C.H.H., Wachter, R., de Weger, L.A., Willems, R., Emberlin, J., 2003. Quantitative trends in annual totals of five common airborne pollen types (*Betula*, *Quercus*, Poaceae, *Urtica* and *Artemisia*), at five pollen-monitoring stations in western Europe. *Aerobiologia* 19, 171–184.
- Stevenson, A.C., 1985. Studies in the vegetational history of S.W. Spain I. Modern pollen rain in the Doñana National Park, Huelva. *J. Biogeogr.* 12, 243–268.
- Sugita, S., 1993. A model of pollen source area for an entire lake surface. *Quat. Res.* 39, 239–244.
- ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca NY, USA.
- Valido, A., Rodríguez-Rodríguez, M.C., Jordano, P., 2011. Interacciones entre plantas y polinizadores en el Parque Nacional del Teide: consecuencias ecológicas de la introducción masiva de la abeja doméstica (*Apis mellifera*, Apidae). In: Ramírez, L., Asensio, B. (Eds.), *Proyectos de investigación en parques nacionales: 2007–2010*. Organismo Autónomo de Parques Nacionales, Madrid, pp. 205–231.
- van der Knaap, W.O., van Leeuwen, J.F.N., Froyd, C.A., Willis, K.J., 2012. Detecting the provenance of Galápagos non-native pollen: The role of humans and air currents as transport mechanisms. *The Holocene* 22, 1373–1383.
- Van der Merwe, J.J.M., Van Wyk, A.E., Kok, P.D.F., 1990. Pollen types in the Lauraceae. *Grana* 29, 185–196.
- Webb, C.J., Shand, J.E., 1985. Reproductive biology of tree lucerne (*Chamaecytisus palmensis*, Leguminosae). *N. Z. J. Bot.* 23, 597–606.
- Webb, T., Laseski, R.A., Bernabo, J.C., 1978. Sensing vegetational patterns with pollen data: choosing the data. *Ecology* 59, 1151–1163.