ORIGINAL ARTICLE

The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands)

Lea de Nascimento[1,2]*, Katherine J. Willis[2,3], José María Fernández-Palacios[1,2], Constantino Criado[4] and Robert J. Whittaker[2]

[1]*Island Ecology and Biogeography Group, University of La Laguna, Canary Islands, Spain,* [2]*Long-term Ecology Laboratory and Biodiversity Research Group, School of Geography and the Environment, Oxford University, Oxford, UK,* [3]*Department of Biology, University of Bergen, Bergen, Norway and* [4]*Department of Geography, University of La Laguna, Canary Islands, Spain*

ABSTRACT

Aim We report the first analysis of the long-term ecology of Tenerife, in order to establish a pre-colonization base-line and to assess the effect of human activity and the role of climatic variation on vegetation during the Late Holocene.

Location A former lake bed in the city of La Laguna (Tenerife, Canary Islands, Spain).

Methods A sedimentary sequence of over 2 m was obtained from the former lake bed. Fossil pollen and microfossil charcoal concentrations were analysed. Radiocarbon dating of the sequence indicates that it spans approximately the last 4700 years. The pollen diagram was zoned using optimal splitting within PSIMPOLL 4.25.

Results Three pollen zones were differentiated: (1) in Zone L1 (*c.* 4700–2900 cal. yr BP) a mixed forest was dominated by *Quercus*, *Carpinus*, *Myrica* and *Pinus*; (2) in Zone L2 (*c.* 2900–2000 cal. yr BP) the laurel forest taxa increased, while *Pinus*, *Juniperus* and *Phoenix* declined; and (3) Zone L3 (*c.* 2000–400 cal. yr BP) was characterized by the decline of *Carpinus* and *Quercus* and the abundance of laurel forest taxa (e.g. *Myrica*). Neither *Carpinus* nor *Quercus* was hitherto considered to be native to the Canary Islands. Their decline started *c.* 2000 years ago, coinciding with microfossil charcoal evidence of increased burning and with archaeological evidence for the first human settlement on Tenerife.

Main conclusions Between *c.* 4700 and 2000 cal. yr BP, the composition of the forest in the valley of La Laguna was very different from what it is at present. In particular, *Quercus* and *Carpinus* appear to have been significant components, alongside components of the present-day laurel forest, and the native pine (*Pinus canariensis*) forest and thermophilous woodland were also more prevalent in the region (but probably not within the lake basin itself) until 3000 cal. yr BP. The subsequent decline of *Quercus* and *Carpinus* led to the establishment of the present laurel forest in the region and a shift to more open vegetation types. These changes indicate that the aboriginal inhabitants of the islands, the Guanches, had a far more profound impact on the vegetation of Tenerife than hitherto realized.

Keywords
Canary Islands, *Carpinus*, forest ecology, Holocene vegetation change, human impact, island ecology, palaeoecology, *Quercus*, Tenerife.

*Correspondence: Lea de Nascimento, Departamento de Ecología, University of La Laguna, Avda. Astrofísico Francisco Sánchez, s/n, La Laguna 38206, Santa Cruz de Tenerife, España.
E-mail: leadenas@ull.es

INTRODUCTION

The Canary Islands constitute an oceanic archipelago of diverse ecosystem types (spanning semi-desert, evergreen forest and alpine desert) and high species endemism, subject to increasing anthropogenic pressures. There are more than 12,500 terrestrial and 5500 marine species in, or around, a land area of only 7500 km[2]. Within this total of 18,000 species,

about 3800 species and 113 genera are endemic (Izquierdo *et al.*, 2004). Among them are many examples of spectacular radiations of animals and plants. There have been many recent studies of the genetics and distributions of endemic Canarian taxa, contributing greatly to the understanding of island evolutionary themes, such as back-colonization, progression rules, multiple invasion, founder effects, adaptive and non-adaptive radiation, and trait shifts (e.g. Juan *et al.*, 2000; Emerson, 2002; Carine *et al.*, 2004; Whittaker & Fernández-Palacios, 2007; Whittaker *et al.*, 2008). These phylogenetic analyses have been aided by the increasingly well specified geological history of the archipelago (Carracedo *et al.*, 1998, 2002); to date, however, there is only a limited Late Quaternary environmental change framework in which to view these phylogenetic studies (Marrero, 2004), and we lack knowledge of the past distributional dynamics of major ecosystem types.

The precise timing of human colonization from Northwest Africa is uncertain, but the sparse archaeological evidence based on mummies suggests a date of around 2500 yr BP (del Arco *et al.*, 1997; Rando *et al.*, 1999; Cabrera, 2001). Hence, human modification of the ecology of these islands significantly pre-dates written records. Castilian settlement followed in the 15th century. The natural vegetation has been heavily modified in all zones, and many species are considered threatened, to the extent that NGOs and governmental organizations alike have prioritized the islands for conservation action (Francisco-Ortega *et al.*, 2000; Whittaker & Fernández-Palacios, 2007; Fernández-Palacios & Whittaker, 2008). These actions have included recent initiatives in forest restoration ecology (http://www.tenerife.es/life/).

This paper addresses the knowledge gap in the long-term ecology of the Canaries by means of palaeoecological analyses of a sedimentary sequence from a former lake bed within the city of La Laguna on the island of Tenerife. We provide a first assessment of the pre-anthropogenic base-line and post-human contact ecological history of the broadleaved forest of Tenerife – a vegetation belt of key biogeographical (e.g. Axelrod, 1975; Bramwell, 1976; Sunding, 1979; Santos-Guerra, 1999; Emerson & Oromí, 2005), functional ecological (Arévalo & Fernández-Palacios, 1998, 2003, 2007; Fernández-Palacios & Arévalo, 1998) and conservation (e.g. Parsons, 1981; Fernández-Palacios & Martín Esquivel, 2001) interest.

The Canary archipelago (Fig. 1) is situated off the hyper-arid coast of Northwest Africa, astride the subtropical high-pressure belt, at the poleward limit of the Hadley Cell (Sperling *et al.*, 2004). The islands form part of the Atlantic island
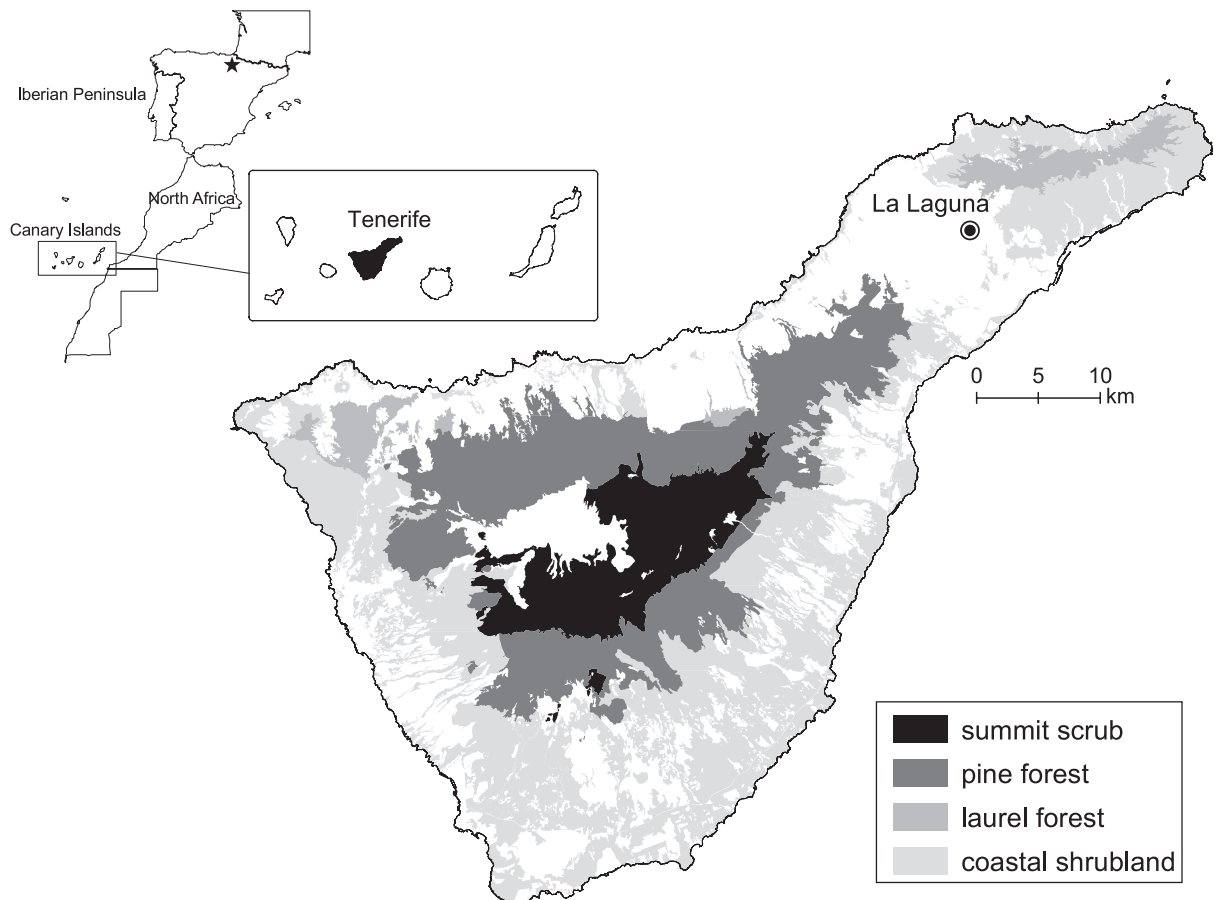

Figure 1 Location of the study site (La Laguna) and the main vegetation types on the island of Tenerife, Canary Islands (adapted from the vegetation map of GRAFCAN, http://www.grafcan.com/). The star symbol indicates the present location of *Carpinus* in the Iberian Peninsula.

biogeographical region of Macaronesia (with the Cape Verde Islands, Madeira, Salvage Islands and Azores), sharing biogeographical affinities with the Mediterranean and Northwest Africa (Whittaker & Fernández-Palacios, 2007). They are true oceanic islands that have never been connected to continental landmasses. They vary in maximum age from 1 to 20 Ma (Carracedo *et al.*, 1998), and phylogenetic data suggest that colonization dates of Canarian lineages span this extended period. The islands remain volcanically active, and over time have been subject to intensive and at times catastrophic erosive and/or volcanic episodes (Canals *et al.*, 2000), which have detectable imprints on the phylogenies of Canarian taxa (e.g. Moya *et al.*, 2004). Tenerife itself dates back to about 11.5 Ma, and for a long time consisted of two or possibly three separate islands (Carracedo *et al.*, 1998, 2002). It is only within the last 1.5 Myr that the great felsic volcanic cycle of Las Cañadas unified the old basaltic massifs of Teno, Adeje and Anaga to form today's island of Tenerife (Anguita *et al.*, 2002). The Canary Islands, inclusive of Tenerife, have thus provided a highly variable physical space assessed over a tectonic time-scale (see Whittaker *et al.*, 2008).

Oceanic islands in the low latitudes are generally considered to have been fairly well buffered from the pronounced climate change of the last 2 Myr. The so-called laurel forests of the Atlantic islands provide a classic illustration in that they are considered to be a Tethyan relictual flora, which colonized from the Mediterranean region during the early Miocene (Axelrod, 1975). This flora and forest type has survived within Macaronesia owing to the persistence of the sub-humid climate on these islands, whereas the flora declined in North Africa and the southern edge of Europe as summer rainfall and winter temperatures decreased (e.g. Axelrod, 1975). As a result, several of the evergreen laurel forest tree species are now considered palaeoendemics (e.g. Sunding, 1979), which is to say that they appear to have persisted relatively little changed on the islands, whereas the original mainland lineages have failed to persist. Examples of Macaronesian taxa recognizable from Tertiary deposits in Europe (5.3 Ma in southern France) include *Laurus novocanariensis*, *Ilex canariensis* and *Picconia excelsa* (Axelrod, 1975; Santos-Guerra, 1999). By contrast, other forest lineages, notably invertebrates, show a far greater degree of *in situ* evolutionary change, or neo-endemism (e.g. see Emerson, 2002; Moya *et al.*, 2004). In short, it has been assumed that the Canary Islands have provided a persistent sub-humid climate over the last several million years, and that this climatic stability has been crucial to the persistence of this forest type and to evolutionary dynamics within this major ecosystem type (Axelrod, 1975; Sunding, 1979; Cronk, 1992). Notwithstanding, changing Pleistocene global climates and associated sea-level change have impacted on the area, elevational range and isolation of the islands, and by inference must have impacted on the distribution and extent of major ecosystem types within the islands (García-Talavera, 1999).

Tenerife encompasses all the main native vegetation types of the archipelago, from the hot, dry semi-desert vegetation of the coastal lowlands (18–21°C, < 250 mm annual rainfall),

through the laurel forest zone (13–16°C, *c.* 1000 mm) and the Canarian pine forest (10–15°C, 400–1000 mm), to the summit scrub (5–10°C, *c.* 400 mm) (Fernández-Palacios, 1992; Fernández-Palacios & de Nicolás, 1995). The laurel forest or *monteverde* occupies an elevational range limited to between 600 and 1200 m a.s.l. on the windward face of the island, and is thought to have once formed a continuous band along the length of the island. The forest is dominated today by some 20 species of evergreen trees. Less than 20% of the estimated pre-human extent of this forest type remains within the archipelago (Fernández, 2001). This forest supports a number of endangered vertebrate and invertebrate taxa. The laurel forest distribution correlates with the zone of cloud formation associated with the trade wind inversion, and at its upper limits (within the Teide massif) this broadleaved evergreen forest gives way to the more xerophytic endemic Canarian pine, forming a taller but naturally less dense coniferous forest. In addition, there are remnant species (e.g. *Phoenix canariensis* and *Juniperus turbinata*) of a presumed sclerophyll, thermophilous woodland zone, downslope of the laurel forest, which was more or less entirely converted to agricultural uses during the historical period (Fernández-Palacios *et al.*, 2004).

A presumed paucity of suitable deposits appears to explain the lack of previous palaeoecological analysis from the Canary Islands. In this paper we report on a sedimentary record spanning the Late Holocene, from a former lake bed in the city of La Laguna, Tenerife. By means of the analysis of fossil pollen and charcoal fragments from a dated core, we set out to (1) establish the pre-settlement ecological baseline, and (2) establish the amplitude of vegetation and environmental variability for the last *c.* 4000 years (i.e. prior to and following human colonization).

MATERIALS AND METHODS

Study site

We extracted a core from a former lake bed in the city of La Laguna (28°30′ N, 16°19′ W), in the north-east of Tenerife. The basin has basaltic bedrock (6–3 Ma) and was formed when a large ravine that once drained the Anaga massif to the west was blocked by the formation of the Cañadas massif, *c.* 1.5 Ma. This resulted in a shallow lake of about 0.5-km diameter, which persisted until about 240 years ago, when water was artificially channelled for agriculture and to prevent flood risk (Criado, 2002). Marshy areas still exist but the lagoon has been encroached on by agricultural land and housing.

The floor of the La Laguna basin is at an altitude of *c.* 560 m a.s.l., and, being influenced by the trade wind inversion, is subject to frequent orographic cloud formation. Mean annual precipitation is about 550 mm, mostly occurring in the winter. Summers are dry and warm. The mean annual temperature is close to 16°C, and the basin is not subject to frost. The soils of the valley have been classified as

Alfisols, suborder Ustalfs. They feature high clay contents and A horizons of 2–6% organic matter (Fernández-Caldas *et al.*, 1982). Climatic and edaphic conditions are appropriate for forest development, but intensive human use over many centuries has limited the recovery and persistence of native vegetation within the study site. The vegetation of the basin today is largely agricultural, with some elements of the xerophytic scrub vegetation on abandoned slopes, and only in the upper reaches of the basin are there remnant stands of laurel forest. Much of the basin is covered by the city of La Laguna itself.

There are two distinct types of native forests nearby, the laurel forest of the Anaga massif (3 km north-east of the site) and the pine forest of La Esperanza Mountain chain (8 km to the west) (Fig. 1). The Anaga laurel forest has some 20 canopy tree species, including four 'palaeoendemic' Lauraceae species (*Laurus novocanariensis*, *Ocotea foetens*, *Persea indica* and *Apollonias barbujana*). Other important species are *Myrica faya*, *Prunus lusitanica*, *Ilex canariensis*, *Ilex perado*, *Erica platycodon* and *Erica arborea* (Arévalo & Fernández-Palacios, 1998; Fernández-Palacios & Arévalo, 1998). The pine forest to the west occupies a band between 1200 and 2000 m a.s.l. on the windward slope, and between 700 and 2300 m a.s.l. on the leeward slope of the island. The canopy of the pine forest is dominated by a single tree species, *Pinus canariensis*, accompanied by several shrub species that constitute the understorey (*Cistus monspeliensis*, *Cistus symphytifolius*, *Adenocarpus viscosus* and *Chamaecytisus proliferus*). Both forest types have been subject to intensive human use. The Anaga laurel forest has persisted within the mountains, reaching its minimum known extent during the 20th century, in connection with the post-Spanish civil war period, since which time it has been allowed to expand a little in area, mainly as a result of the abandonment of agriculture (Fernández-Palacios *et al.*, 2004). The pine forest was also greatly reduced in extent in the historical period by the need for wood for a variety of purposes (especially for sugar manufacturing in the first century of Spanish establishment) and later by the use of land for agriculture and livestock, and by intense fires (Parsons, 1981). After four centuries of continued exploitation, replanting efforts were undertaken in the second half of the 20th century (Ceballos & Ortuño, 1976).

Sample collection and analyses

A 2.15-m sediment core in 0.5 m sections was collected from Massanet point, La Laguna, (28°29′32″ N, 16°19′06″ W) using a 5-cm diameter modified Livingstone piston corer (Wright, 1967). The core was extruded in the field, wrapped in cling-film and aluminium foil, and transported back to the Long-term Ecology Laboratory, Oxford University Centre for the Environment, for analyses. In the laboratory, 1-cm^3 subsamples of sediment were extracted down the core using a volumetric subsampler. The whole sequence was subsampled at a 4-cm interval starting at 1 m. Three sedimentary samples (covering a depth of *c*. 1 cm for each sample) were also taken

for ^{14}C Accelerator Mass Spectrometer dating (carried out by Poznan Radiocarbon Laboratory, Poland).

Extraction of pollen from the sediment samples followed standard procedures (summarized in Bennett & Willis, 2001) and involved the addition of acids to remove the carbonates, of alkali and acetolysis to remove humic acids and polysaccharides, and of hydrofluoric acid to remove silica and silicates. The pollen remaining in the sample was then stained and mounted in silicone oil for identification and counting. Exotic *Lycopodium* tablets of a known concentration were added in order to determine the concentration of pollen and microfossil charcoal (Stockmarr, 1971). Identification of the pollen in the samples was carried out by reference to various keys and photographs (e.g. Reille, 1992, 1995, 1998) and to pollen reference material from Europe, Africa and the Canary Islands in the collection of the Oxford Long-term Ecology Laboratory. Nomenclature for plant vascular species follows Izquierdo *et al.* (2004). In order to ensure a statistically significant sample size (Maher, 1972), a minimum of 300 pollen grains were counted for each level analysed.

Samples for microfossil charcoal analysis were prepared as part of the routine pollen analysis (Whitlock & Larsen, 2001), and the charcoal concentration in each sample was determined using the point count method (Clark, 1982). This provides an estimate of the area of charcoal covering each slide counted. By assessing this measurement against the exotic pollen count, a measure of charcoal concentration (cm^2 cm^{-3}) per sample was obtained.

Data handling

A number of data-handling techniques were employed in order to compare and contrast the radiocarbon dates and the pollen and microfossil charcoal data sets, as follows.

The radiocarbon dates were calibrated using the program INTCAL98 (Stuiver *et al.*, 1998) and subsequently labelled as cal. yr BP. The relationship between age and sediment depth was modelled using a linear interpolation model, in which estimated deposition times were calculated for the gradients between adjacent pairs of points (Bennett, 1994). This enabled calculation of interpolated ages for intermediate depths.

The raw pollen data were converted to pollen percentage values (% total pollen) using a pollen sum based on the sum of total arboreal pollen (AP) and non-arboreal pollen (NAP), excluding spores and hygrophytes. The pollen percentage data were then plotted against age and depth using the plotting program PSIMPOLL 4.25 (Bennett, 2005). The same program also enabled the plotting of the microfossil charcoal results (expressed as cm^2 cm^{-3}). For ease of description, the pollen diagram was zoned using optimal splitting (Birks & Gordon, 1985; Bennett *et al.*, 1992) within the PSIMPOLL program (Bennett, 2005). This divides the diagram into a given number of zones in such a way as to minimize the total variance for that number of zones. A determination of the number of significant zones was calculated using a broken-stick model (Bennett, 1996).

Table 1 Radiocarbon dates from three levels in La Laguna sediments.

Depth (cm)	Laboratory code	Age (^{14}C yr BP)	Calibrated age (cal. yr BP)
146	POZ-13147	2045 ± 30	1993 ± 38
180	POZ-13148	3075 ± 35	3304 ± 46
200	POZ-13149	3745 ± 35	4099 ± 55

RESULTS

Chronology

Three radiocarbon dates were obtained from the sequence (Table 1). These indicate that the sedimentary sequence collected from La Laguna represents a period of *c.* 4300 years, spanning from 4700 ± 40 to 380 ± 38 cal. yr BP. The uppermost metre of sediments contained pollen that was too highly degraded to be included in the analysis.

The stratigraphy of sediments (Fig. 2) was almost homogeneous along the core (100–214 cm), composed of brown and grey clays containing some organic material. A difference in composition was observed at the bottom of the core (214–220 cm) owing to the presence of finely laminated lake marl with low clay content. There were no plant macrofossils or identifiable (macroscopic) charcoal fragments in the sediments analysed.

Pollen

The results obtained from the 28 samples analysed are presented in a series of pollen percentage diagrams (Figs 2–4). Optimal splitting of the pollen percentage diagram showed three zones: L1 (215–170 cm) spanning from *c.* 4700 to 2900 cal. yr BP; L2 (170–145 cm), from *c.* 2900 to 2000 cal. yr BP; and L3 (145–103 cm), from *c.* 2000 to 400 cal. yr BP. Throughout the sequence, arboreal pollen is the most abundant type, indicating that a forested landscape predominated around the basin in the last 5000 years (Fig. 4).

Zone L1 (c. 4700–2900 cal. yr BP)

In the lowermost zone (Fig. 2), percentages of arboreal pollen indicate that a mixed forest containing *Quercus*, *Carpinus*, *Pinus* and *Myrica* was present in the region around the basin.
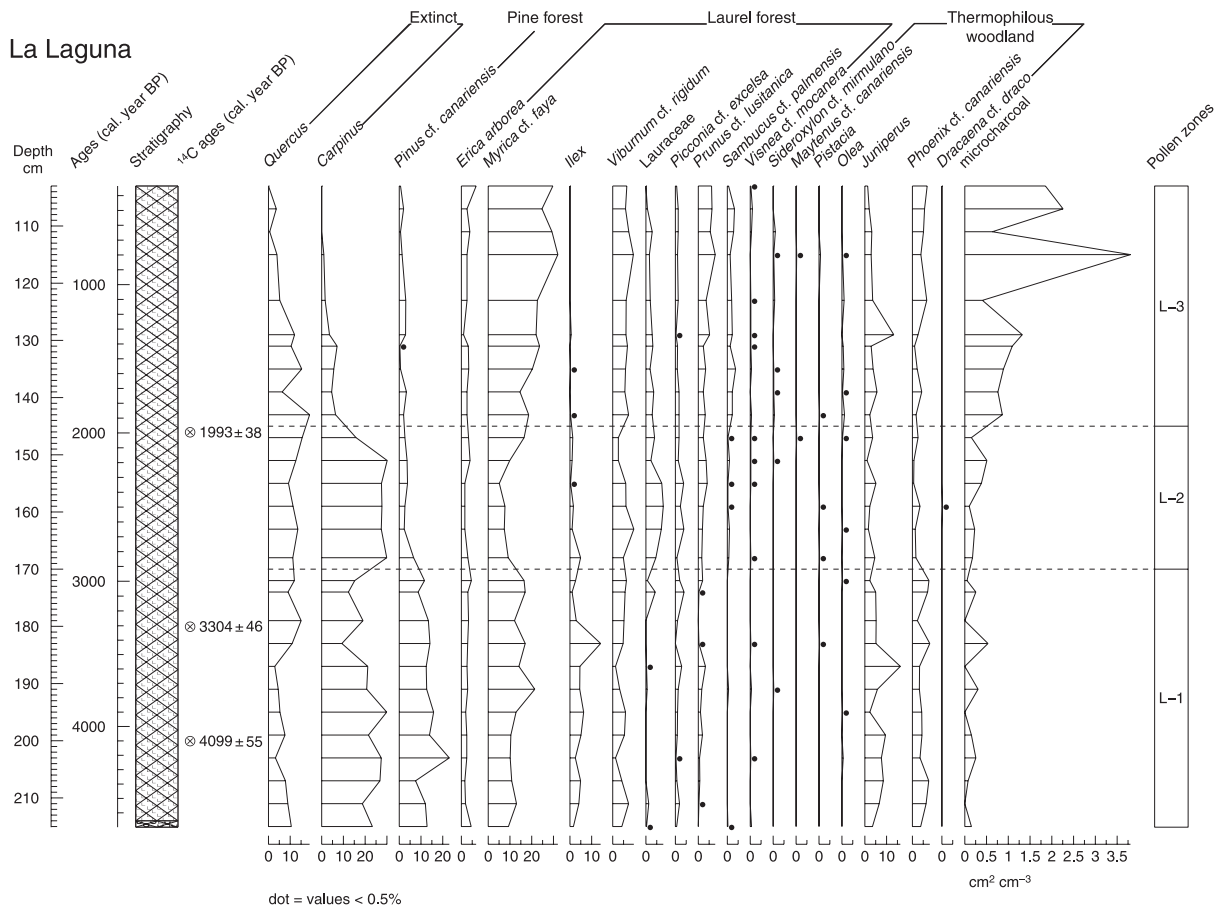

Figure 2 Pollen diagram for sediments of La Laguna, with trees ordered by the forest type to which they belong at present. Percentage pollen abundance and micro-charcoal concentration are plotted against age (cal. yr BP). The dashed lines indicate the zones delimited by numerical zonation (optimal splitting within PSIMPOLL 4.25).
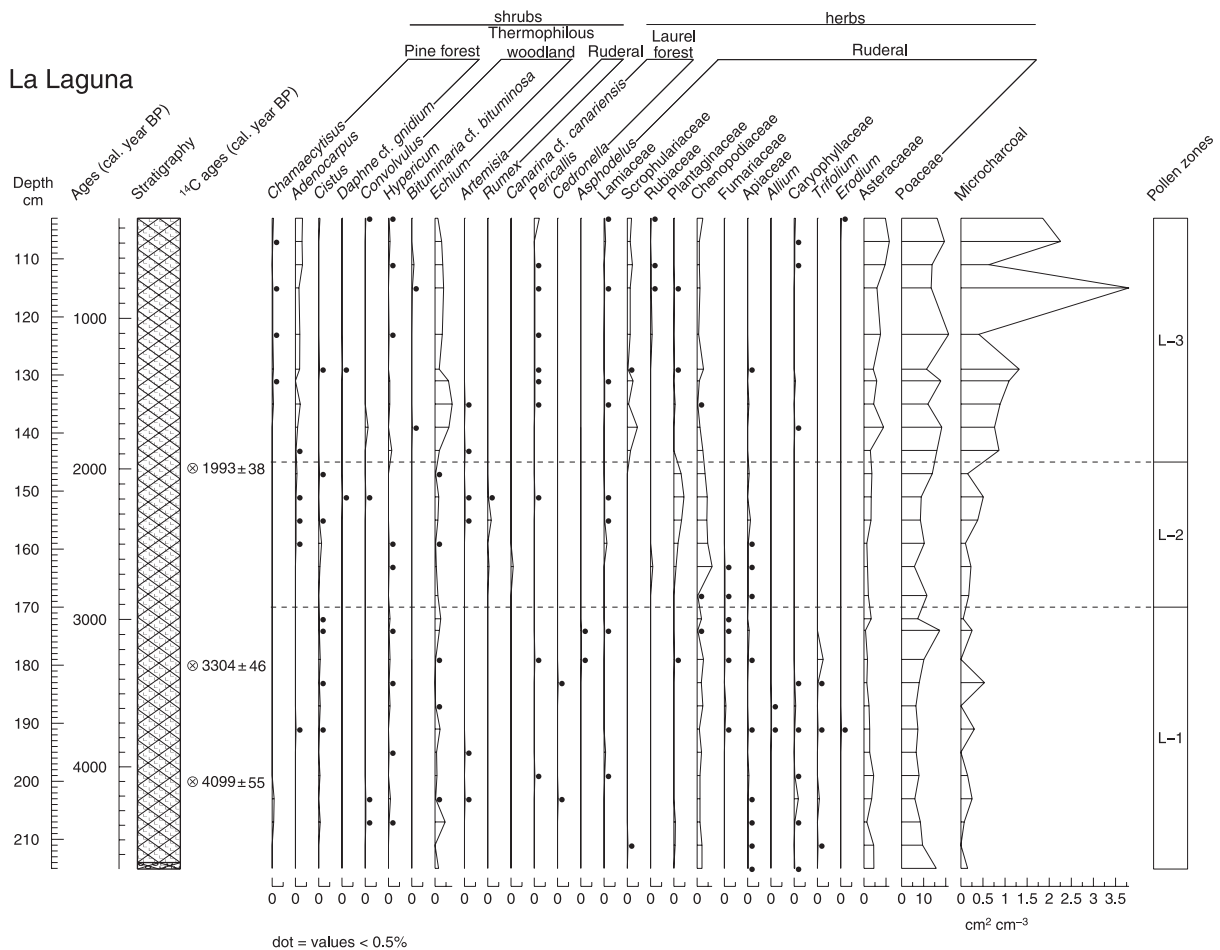
Figure 3 Pollen diagram of La Laguna, with shrubs and herbs ordered by the vegetation type to which they belong. Percentage pollen abundance and micro-charcoal concentration are plotted against age (cal. yr BP). The dashed lines indicate the zones delimited by numerical zonation (optimal splitting within PSIMPOLL 4.25), as shown in Fig. 2.

The presence of *Quercus* and *Carpinus* is particularly interesting because neither of these tree taxa was hitherto thought to have been part of the native vegetation in the Canaries. It is unclear from the pollen morphology what species these are. It may reasonably be assumed that pollen of *Pinus*, *Myrica*, *Picconia*, *Prunus*, *Viburnum*, *Sambucus*, *Visnea*, *Sideroxylon*, *Maytenus*, *Phoenix* and *Salix* coincide with the only native species of these genera that occur on Tenerife. Although there is a second Canarian *Myrica* species (*M. rivas-martinezii*) growing in the three westernmost islands of the archipelago (La Palma, La Gomera and El Hierro), it is nowadays extremely rare on those islands and absent from Tenerife. The same applies to *Dracaena tamaranae*, which is present only on the island of Gran Canaria. In the case of *Erica arborea*, the pollen could be differentiated from that of other species of Ericaceae that are native to the island (*Erica platycodon* and *Arbutus canariensis*). In contrast, pollen from species of Lauraceae (*Apollonias barbujana*, *Laurus novocanariensis*, *Ocotea foetens* and *Persea indica*), *Ilex* (*Ilex canariensis* and *Ilex perado*) and *Juniperus* (*Juniperus*

cedrus and *Juniperus turbinata*) could not be discriminated to the species level.

Other taxa present in this pollen zone, but in lower abundances, include *Phoenix canariensis* and *Juniperus*. Several other taxa that currently occur in the evergreen laurel forest were recorded, including *Viburnum rigidum*, *Erica arborea*, *Prunus lusitanica*, *Picconia excelsa* and *Ilex*. It is probable that most of the species from the laurel forest are under-represented in the pollen record because they are entomophilous (i.e. insect-pollinated). Shrubs are scarcely represented in this pollen zone (Fig. 3). Those that are include *Echium* and *Hypericum*, which are presently found at the transition between evergreen and thermophilous forests, and *Cistus*, which is found in the pine forest understorey and in disturbed sites. Herbaceous taxa present (Fig. 3) include the Poaceae, Asteraceae and Chenopodiaceae families, but they account for less than 20% of the total pollen sum, suggesting a predominantly forested environment. Hygrophytes such as *Ranunculus*, *Carex*, *Salix canariensis* and ferns (Fig. 4) were also very abundant during this period, probably
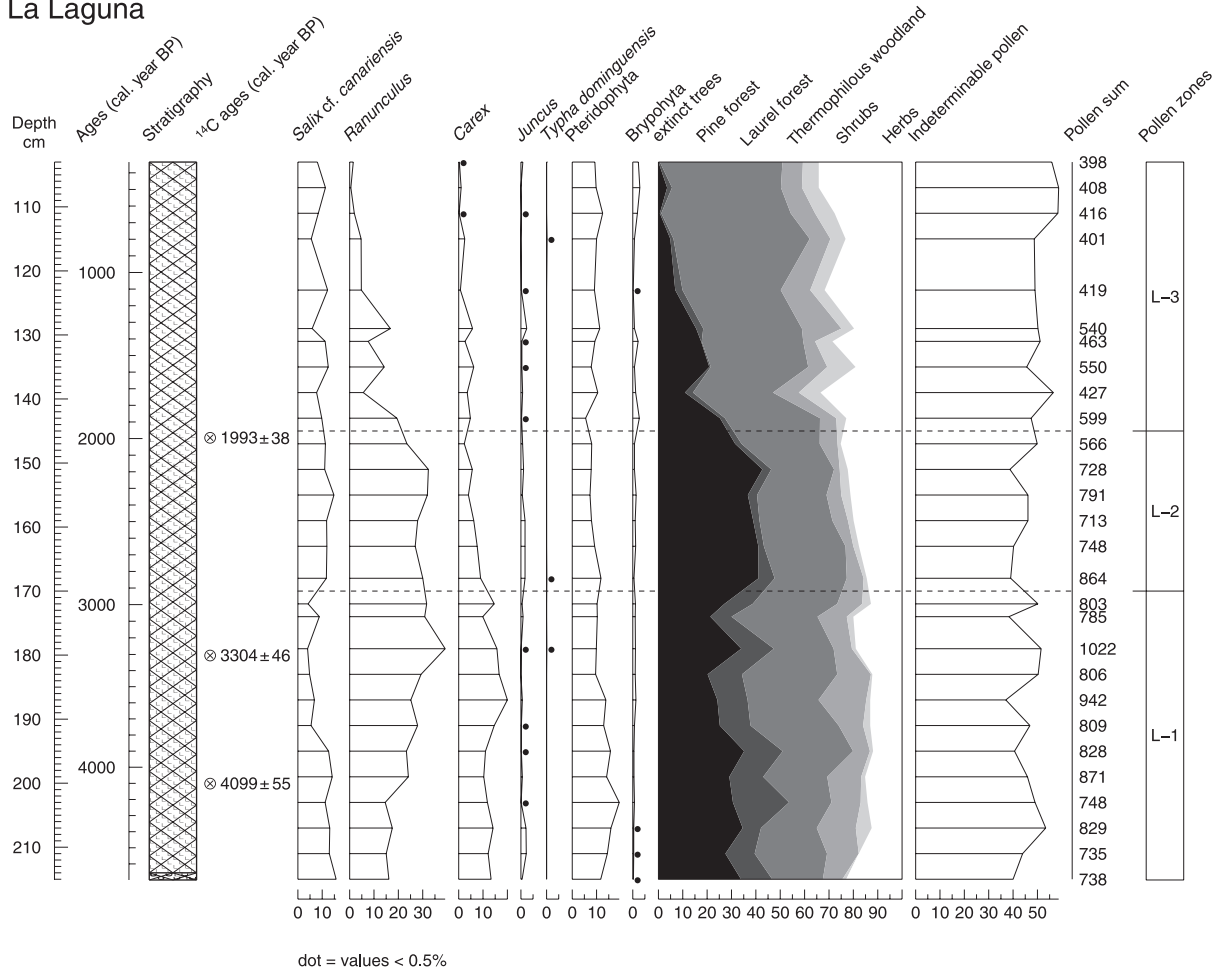
La Laguna

Figure 4 Pollen diagram of La Laguna, with hygrophytes and total pollen sums for trees (divided into main forest types), shrubs and herbs. Percentage pollen abundance is plotted against age (cal. yr BP). The dashed lines indicate the zones delimited by numerical zonation (optimal splitting within PSIMPOLL 4.25), as shown in Fig. 2.

growing in the margins of the basin and related to the existence of a permanent lake.

Zone L2 (c. 2900–2000 cal. yr BP)

In this zone, the composition of arboreal pollen (Fig. 2) suggests the presence of a mixed forest where the dominant tree taxa were *Quercus*, *Carpinus*, *Myrica*, Lauraceae species and *Viburnum*. A change in the abundance of some taxa in comparison with the previous period can be observed. There was a decrease of pollen percentage for *Pinus*, *Myrica*, *Ilex*, *Juniperus* and *Phoenix*, whereas *Erica* maintained a similar percentage value to that in the previous zone. In contrast, Lauraceae, *Viburnum*, *Picconia* and *Prunus* became more abundant and consistent during this period. The composition and abundance of shrubs in this zone (Fig. 3) were very similar to those in zone L1. The best-represented shrubs were *Cistus*, *Adenocarpus*, *Echium* and *Hypericum*. In the herbaceous pollen (Fig. 3), Chenopodiaceae and Plantaginaceae taxa increased, but herbaceous pollen continued to represent a low, if

growing, percentage of the total pollen sum. Hygrophytes were very abundant in this zone, indicating the persistence of the lake during this period.

Zone L3 (c. 2000–400 cal. yr BP)

This period is characterized by the decline of *Carpinus* pollen and a corresponding increase of *Myrica* pollen, indicating a change in the forest composition 2000 years ago (Fig. 2). *Carpinus* totally disappeared from the sequence *c.* 700 cal. yr BP, whereas *Quercus* was still present until the end of the period, although with low values. By 700 years ago, the forest around the basin contained mainly *Myrica*, *Erica*, *Viburnum*, *Prunus*, *Sambucus*, Lauraceae and *Quercus*, suggesting that a forest similar to current evergreen laurel forest (with the exception of *Quercus*) became established in the region during this period. *Pinus*, *Juniperus* and *Phoenix* pollen percentages continued to show a low but persistent presence in this period.

The increase of shrubs in zone L3 (Fig. 3) is attributable mostly to a higher percentage of pollen from *Echium* and

Adenocarpus, both taxa commonly found in the belt of vegetation that surrounds the laurel forest. *Erica arborea* and *Myrica faya* accompany these shrubs, forming a community of transition between the laurel forest and the communities growing below and above it. An increase in grasses (Poaceae) and other herbaceous taxa (Asteraceae, Rubiaceae or Scrophulariaceae families) is also observed in this zone of the diagram (Fig. 3). The decrease of hygrophytes (Fig. 4) indicates the decline in the water level that changed the lake into a shallow and seasonal pool.

Microfossil charcoal

Results from the microfossil charcoal record are presented in Figs 2 and 3. In zones L1 and L2, covering the period from 4700 to 2000 cal. yr BP, the input of microfossil charcoal to the basin was relatively low, and can be taken to be indicative of the natural burning frequency of the forest. With the start of zone L3, from 2000 cal. yr BP, a significant increase in microfossil charcoal concentration occurred, the date coinciding with the first evidence for human occupation of the island (which is not to say that humans may not have colonized somewhat earlier than so far established).

DISCUSSION

Climate in the region over the past 5000 years

Palaeoclimatic data in the Canaries are scarce and relate mainly to the last glacial and interglacial periods. Based on geomorphological and sedimentological data there is evidence of trade winds circulation since the Early Holocene (Coudé-Gaussen & Rognon, 1993). Based on the occurrence of landslide activity in the Canaries during the Holocene, Lomoschitz *et al.* (2002) suggested that the present interglacial in the Canary Islands and Northwest Africa has included humid and wet episodes. Moreover, aeolian deposits in Fuerteventura, which is nowadays the most arid island in the archipelago, contain interbedded levels of land snail shells, insect brood cells and alluvial deposits that indicate humid phases within the subtropical arid climate during the Holocene (Meco *et al.*, 1997). This general lack of palaeoclimatic data in the Canaries, in particular for the last 5000 years, makes it necessary to search for palaeoclimatic variations in the records available from nearby regions such as Northwest Africa and the Iberian Peninsula.

Climate during the Early to Middle Holocene (mainly during the interval 8000–6000 yr BP) in northern Africa has been described as a period of moister conditions (Lamb *et al.*, 1989; Hooghiemstra *et al.*, 1992; Jolly *et al.*, 1998; Gasse, 2000; Prentice *et al.*, 2000). From *c.* 5000 to 4000 years ago a shift towards a warmer and drier climate occurred in northern Africa and the western Mediterranean. A progressive desiccation, suggested by changes in lake levels, supports the idea of a general trend to climatic aridification, from eastern to western regions, over the second half of the Holocene (Damnati, 2000; Magny *et al.*, 2002). Pollen records of many regions of the Iberian Peninsula show this period of increasing aridity, generally characterized by a decline in deciduous and mesophilous taxa (favoured by cooler and moister conditions during the Middle Holocene) vs. an increase in xerophytes and the spread of present Mediterranean-type forest (Yll *et al.*, 1997; Jalut *et al.*, 2000; Carrión *et al.*, 2001a,b, 2003a, 2004; Carrión, 2002; Pantaleón-Cano *et al.*, 2003).

The region of Maghreb in Morocco apparently maintained wetter conditions from 6000 to 4000 yr BP, as evidenced by pollen records, plant macrofossils and sedimentological data (Rognon, 1987; Cheddadi *et al.*, 1998). Moreover, it is difficult to recognize any natural trend to aridification as mentioned above because of confounding human interference with vegetation over the last 4000 years. The reconstruction of climate in Morocco based on the identification of the closest modern analogues of fossil pollen (Cheddadi *et al.*, 1998) shows a clear difference between the Early and Late Holocene. At *c.* 6500 yr BP there was a transition from warm and dry to cooler and moister conditions, which were maintained during the last phase of the Holocene. Superimposed on the long-term climatic trend are several shorter arid events, inferred from the intermittent occurrence of shallow-water facies (Lamb *et al.*, 1991).

The results described for La Laguna indicate that the climate in the studied region could have been very similar to that obtained for the Atlas in Morocco by Cheddadi *et al.* (1998). A first period spanning *c.* 4700–2900 cal. yr BP was dominated by taxa requiring humid conditions (*Quercus*, *Carpinus*, *Myrica*, *Viburnum*, *Erica*, *Prunus*, *Picconia*, *Ilex*, etc.) and therefore probably influenced by the trade winds. There are also xerophytic trees (*Pinus* and *Juniperus*) during this interval of 2000 years, indicating the presence of pine forest and thermophilous woodland in the region around La Laguna.

In the following period, *c.* 2900–2000 cal. yr BP, xerophytic forest species were still present in the landscape, but the proportion was lower, and the mixed forest became even more dominant. As we have seen above, there was a general trend to aridification during the Late Holocene in many Mediterranean regions, but this trend is not confirmed by the pollen record in La Laguna. Here, instead of a substitution of mesophytic vegetation by taxa indicative of xerophytic vegetation, the dominance of the mixed humid forest becomes more evident.

As true elsewhere, for example in the Middle Atlas (Lamb & van der Kaars, 1995), the climatic trend of the last 2000 years cannot readily be interpreted from the pollen fossil record at La Laguna because the role of human impact on the vegetation, as inferred from the disappearance of some tree taxa and the increased fire regime, confounds attempts to link pollen depositional changes solely to natural forcing.

The impact of human activity

Authors do not agree on a precise date for the arrival of the aboriginal Guanche population on the Canaries, but it is estimated to have occurred *c.* 3000–2000 years ago (Parsons, 1981; del Arco *et al.*, 1997; Rando *et al.*, 1999). The Guanches

were mainly goatherds, but they also introduced other domestic animals such as sheep, pigs, dogs and cats, whereas crop cultivation was a secondary activity. Some accounts from the time of the Conquest by the Castilians at the end of the 15th century refer to the use of the former lake in La Laguna by the aborigines and their animals as a watering place (Criado, 2002). The Guanches probably used open areas for grazing but they also moved their livestock from the coast to the mountains, depending on the season, in search of green pastures. The continued use of the lake as a pond for animals in transit implies an impact on the vegetation not only by goats and sheep but also by pigs, which like eating roots, acorns and other fruit.

Although archaeological studies have claimed that the Guanches had poor technological development and were adapted to and dependent on the environment (Machado & Ourcival, 1998), work elsewhere has established that such societies could well have changed the composition of the forest and even have caused the disappearance of trees and/or of particular tree species (e.g. Bahn & Flenley, 1992; Diamond, 2005). The abrupt shift in microfossil charcoal concentration shows how burning has increased markedly over the last 2000 years. Other anthropogenic indicators become evident during the third zone in the diagram: examples include several nitrophilous taxa (Rubiaceae, Plantaginaceae, Apiaceae) and fodder shrubs (Bituminaria). The clearance of the forest is also signalled by the slight increase in shrubs and herbaceous taxa (Adenocarpus, Artemisia, Chamaecytisus, Cistus, Convolvulus, Echium, Hypericum, etc.), most of them occurring in the communities that have substituted for the former forest cover.

As shown by the total sum, arboreal pollen was dominant during the whole sequence at La Laguna (Fig. 3), denoting the continued presence of forest within the region during the last 5000 years. However, the specific composition of this forest has undergone two notable shifts during the studied period. The first change, at around 2900 cal. yr BP, may well be attributable to a climatic switch from drier to humid conditions, as explained above. The second change occurred c. 2000 cal. yr BP, and is much the more drastic, as two tree taxa (Quercus and Carpinus), which had been dominant components since at least the start of our record, c. 4700 cal. yr BP, progressively vanished from the sequence. This change in forest composition coincides with archaeological evidence for the first human settlements, thus supporting the interpretation that this transition was driven by human influences, such as forest clearance, grazing, or altered fire regimes. Although historical documents do not provide evidence of a systematic management of the forest, or of the purposeful use of fire (Galván, 1993), the high concentrations of microfossil charcoal suggest that the Guanches used fires to clear forested vegetation in order to provide pastures and land for agriculture.

It is thought that the Guanches were wholly or partly responsible for the extinction of several Canarian animals (Cabrera, 2001; Rando, 2002; Bocherens et al., 2006; Rando & Alcover, 2008). Their role in the extinction of plant species is, however, unknown. Although many Canarian endemic species have been reduced to small populations by the effect of grazing during the historical period (Nogales et al., 1992; Rodríguez-Piñero & Rodríguez-Luengo, 1993; Francisco-Ortega et al., 2000) it is difficult to identify whether the damage was caused largely by the Pre-Hispanic grazing culture, the post-Conquest culture, or a combination of both.

The decline of Carpinus occurred in a period of only about 400 years, and it disappeared altogether within an interval of 1200 years, whereas the initial Quercus decline, associated with the putative time of human colonization, was far less pronounced, although it too had essentially dropped out of the record by the end of the Conquest. The speed with which both tree taxa disappeared is a clear sign of the influence of humans in the process (Arroyo et al., 2004). As both Carpinus and Quercus are valuable sources of fuel, wood and fodder, it may be that a selective removal and/or suppression of these trees was practised, at least during the first centuries of pre-Hispanic settlement. The selection of these trees within the forest might have happened because the colonists knew the species and were more familiar with them (Quercus occurs in Northwest Africa, although Carpinus does not), because they grew close to their settlements, or because their properties were valued for specific uses. For instance, the reduction of Quercus canariensis to small stands in the Middle Atlas region since c. 2500 yr BP is attributed to the exploitation of the area by humans (Lamb & van der Kaars, 1995). The inability of many species of Carpinus and Quercus to reproduce vegetatively (Tutin et al., 1964) could be another reason for a relatively fast decline of these trees. The predation of acorn fruits by frugivorous animals and seedling mortality as a result of herbivory have been shown to be important main causes for regeneration failure in many oak species in other settings (Crawley & Long, 1995; Herrera, 1995; Leiva & Fernández-Alés, 2003). Possibly, a superabundance of ungulates (goats, sheep and pigs introduced by the Guanches) could have had a harmful effect on the regeneration of Quercus on Tenerife.

The corresponding increase in pollen from Myrica faya during the decline of Carpinus and Quercus is evidence of the expansion of the characteristic Erica–Myrica woody heath that appears after natural or human disturbances of the laurel forest and the consequent conditions of increased light (Fernández-Palacios & Arévalo, 1998). Initial canopy opening is also linked to an increase in grasses (Poaceae).

Many historical documents about the arrival of the first Castilians conquerors on Tenerife, in AD 1494, describe the valley of La Laguna as a densely forested area, mentioning some trees, such as Erica arborea, Visnea mocanera and Arbutus canariensis, growing around the pool (Criado, 2002). Our results show how for the last 2000 years the dominant formation within the region has been very similar in composition (Lauraceae, Myrica faya, Erica arborea, Viburnum rigidum, Prunus lusitanica and Picconia excelsa) to the laurel forest we know today, and not very different from that described by the first historians. Since the arrival of the first European colonizers, the former lake and the region around it

have been used for a variety of purposes. The use of land for grazing, the need for fuel and wood for construction, and the expansion of agriculture accelerated the process of erosion, affecting the surrounding slopes of La Laguna valley, as described in many historical records (Criado, 2002), and had much to do with the shallowing of the lake. The acceleration in the sedimentation rate probably occurred in the last 500 years, in large part as a consequence of the rapid deforestation in the basin. Some indicators of the desiccation of the lake are evident within the last 2000 cal. yr BP, as exemplified by the increase in Asteraceae (probably growing in the desiccated margins) and by the significant reduction in pollen from hygrophytes.

The lost trees of the forest of La Laguna

The two lost genera (*Quercus* and *Carpinus*) were components of the Pliocene floras of southern Europe, along with other elements of the laurel forest such as *Ilex*, *Viburnum*, *Prunus*, *Picconia*, *Erica*, *Myrica* and species of Lauraceae (Axelrod, 1975; Santos-Guerra, 1999). The abundance of these taxa is probably underestimated in the pollen diagram (Fig. 2) for two reasons: (1) insect-pollinated species produce less pollen than wind-pollinated ones (*Pinus*, *Myrica*, *Quercus*, *Carpinus*, etc.), and (2) Lauraceae pollen grains are easily fragmented during sample preparation (especially during acetolysis) (Bennett & Willis, 2001). The analysis of modern pollen rain in different communities will help to refine the interpretation of Canarian fossil pollen diagrams in the future.

During the Late Miocene and Pliocene, many of the Canarian taxa that make up the laurel forest were distributed in the Mediterranean Basin adjacent to coniferous and deciduous forests that are absent in the Canaries but that are distributed through temperate parts of the Holarctic ecozone (Axelrod, 1975; Milne, 2006). The temperate alliance was one of the Pliocene floras of southern Europe that lived close to or with members of the Canarian laurel forest in the Mediterranean province. *Carpinus* is nowadays distributed mainly in eastern and central Europe, with an isolated area of distribution in the Iberian Peninsula (2000 km from Tenerife; see Fig. 1) at the western limit of the Pyrenees chain (Aizpuru & Catalán, 1984). *Carpinus* is absent from most Holocene palynological records of the Iberian Peninsula (Peñalba, 1994; Carrión *et al.*, 2003b), although its presence has been detected in pollen records of the Cantabrian–Atlantic territories (Ramil-Rego *et al.*, 1998), suggesting the existence of Pleistocene refugia. Other palynological records from previous periods show the presence of *Carpinus* in the Iberian Peninsula during the last glaciation (Burjachs & Juliá, 1994; Sánchez Goñi *et al.*, 1999; Yll *et al.*, 2003; Burjachs, 2006; Gómez-Orellana *et al.*, 2007). During interglacial periods, *Carpinus* appears to have spread north, late in the succession, from its refugia in the Balkans and southern Italy (Bennett *et al.*, 1991; Willis, 1994; Tzedakis *et al.*, 2002; Grivet & Petit, 2003). The physical barrier of the Pyrenees, as suggested by Turner & Hannon (1988), or

human action during the Late Holocene (Peñalba, 1994) could have marked a limit to its distribution in the east of the Iberian Peninsula in the transition of the last glacial/interglacial.

From our results we can only confirm the presence of *Carpinus* on the island of Tenerife during the last *c.* 4500 years. Therefore its early origin as one of the surviving elements of the Neogene flora from the Tertiary period in the Canary Islands is, at this stage, only a possibility. In this case *Carpinus* could have persisted in the Canaries during the Pleistocene, where climatic oscillations are thought to have been less pronounced than in the south of the Iberian Peninsula and Northwest Africa. Then, during the Late Holocene, the impact of the first human colonists, in time, caused its disappearance from the islands.

Typical broadleaved sclerophyllous taxa of the Mediterranean, such as *Quercus* species, which were hitherto not considered part of the native Canarian flora, were also part of the Neogene flora living together with Canarian taxa in the Mediterranean region (Axelrod, 1975). In contrast to the absence of *Carpinus*, there are many records of *Quercus* species in the Iberian Peninsula (e.g. Pons & Reille, 1988; Stevenson & Moore, 1988; Carrión & Dupré, 1996; Carrión *et al.*, 2001a,b, 2003a, 2004; Carrión, 2003; Pantaleón-Cano *et al.*, 2003; Riera, 2006) and in Northwest Africa (Lamb *et al.*, 1991; Marret & Turon, 1994; Lamb & van der Kaars, 1995) during the Holocene. In the records from the South Iberian Peninsula, deciduous taxa of *Quercus* showed an optimum during the Middle Holocene, being replaced by evergreen *Quercus* in the Late Holocene. In Northwest African records, both evergreen and deciduous *Quercus* were very abundant in the Early Holocene, although deciduous taxa declined during the Late Holocene in favour of the evergreen types. *Quercus* grains in the La Laguna record were identified only to the level of genus, and because the pollen was not very well preserved we could not match it with the evergreen or deciduous type.

Nowadays several species of deciduous [i.e. *Q. canariensis* (see below), *Q. faginea*, *Q. pubescens*, *Q. pyrenaica*, *Q. suber*] and evergreen (i.e. *Q. coccifera*, *Q. ilex*, *Q. rotundifolia*) oaks are part of the xerophyllous and deciduous forests distributed through the Iberian Peninsula and northern Africa. As proposed for *Carpinus* (above), *Quercus* could have been a member of the Neogene relict flora that managed to survive in the Canary Islands with other laurel forest taxa. Presciently, Axelrod (1975) raised the question of how the species of Lauraceae, with fruits and seeds of large size, had managed to colonize the islands, whereas none of the species of *Quercus*, which were associated with Lauraceae species in the Mediterranean Pliocene, had done so. Other authors described the laurel forest as an impoverished relict of mixed oak–laurel forest deriving from the early Neogene and attributed its deterioration to human impact during the Late Holocene (Höllermann, 1981). On the island of Madeira (within the Macaronesian region and only some 500 km northwards of Tenerife), Sziemer (2000) reported the presence of several tree

species, now extinct, such as *Ulmus minor*, *Corylus australis*, *Ilex hartungi* and *Frangula azorica*, among other tree species still inhabiting the island's laurel forest (*Clethra arborea*, *Erica arborea*, *Vaccinium padifolium*, *Laurus novocanariensis* or *Myrica faya*) in the Late Pliocene deposits of Sao Jorge. Laurophyllous *Quercus* were also members of the oak–laurel forests or evergreen sclerophyllous–laurophyllous forest in the Catalonian basin during the Oligocene and Miocene (Sanz de Siria, 1987, 1992). To date it has been assumed that these tree species were not able to migrate during colder periods and overcome the barrier posed by the Mediterranean (Barrón *et al.*, 2003; Barrón & Peyrot, 2006), but our results show the possibility of the presence of laurophyllous *Quercus* in the Canary Islands even though these species failed to persist in the Iberian Peninsula.

Specific mentions of *Quercus* from the Canary Islands in records from the historical period (i.e. the last 500 years) generally assume the genus to have been introduced by people (Izquierdo *et al.*, 2004). Several historians and naturalists mentioned the early (i.e. early in the Castilian period) presence of some species in the Canary Islands, including *Q. canariensis*, *Q. ilex*, *Q. lusitanica*, *Q. suber* and *Q. robur*, in particular on the island of Tenerife (Salas & Cáceres, 2000). These observations probably refer (mostly) to trees introduced by colonizers shortly after the conquest. Although the name *Q. canariensis* refers clearly to a Canarian distribution, there is no certain evidence of the natural presence of this species in the islands, and it is presently distributed in the Iberian Peninsula and northern Africa. Its name has been attributed to a presumed mistake in the labelling and description of the species, which was first collected and labelled by the French naturalist Broussonet and later described by the German botanist Willdenow (Do Amaral Franco, 1990). Stands of *Q. canariensis* in the Iberian Peninsula (Blanco *et al.*, 1997) share common taxa with the Canarian laurel forest, including *Prunus lusitanica*, *Viburnum rigidum*, *Erica*, *Laurus* and *Ilex*, all of them recorded in the pollen sequence from La Laguna. However, we cannot deduce from our results if the *Quercus* pollen were *Quercus canariensis* or a different type or types of oak.

Although macrofossils were not retained from the sediments of La Laguna, there are other sites on the island of Tenerife (caves located in the north of the island) that have been studied for macrofossils, in particular fragments of macroscopic charcoal (Machado *et al.*, 1997; Machado & Ourcival, 1998). Anthracological fossils were found for several taxa from the laurel forest (i.e. *Laurus novocanariensis*, *Apollonias barbujana*, *Ilex canariensis*, *Erica*, *Myrica faya*, *Salix canariensis*), from the pine forest (*Pinus canariensis*) and from thermophilous woodland (*Juniperus*). Fragments of charcoal from *Carpinus* or *Quercus* were not identified. This could be explained by two factors: (1) the oldest sequence analysed by Machado *et al.* (1997) extends back only to *c.* 250 yr BC, coinciding with the beginning of the decline of both taxa, and therefore the trees might have been less abundant during that period; and (2) the archaeological sites

studied are located *c.* 30 km from La Laguna, and both tree taxa may have been absent from that region as vegetation zonation is pronounced on Tenerife owing to the strength of the climatic gradients across the island. Consequently, although anthracological data for the north of Tenerife do not show evidence of the presence of *Quercus* and *Carpinus*, they do not necessarily contradict the fossil pollen record from the old lake of La Laguna.

These first results raised from the palynological record of the former lake of La Laguna were unexpected. A key finding of this analysis is that two tree genera lacking from the currently recognized native flora, namely *Carpinus* (no previous record) and *Quercus* (native status previously disputed), were important constituents of the forest in the La Laguna basin prior to human settlement. Our results have important implications for conservation (cf. Willis & Birks, 2006) and suggest the possibility of a lost forest type or subtype, and they demand a reappraisal of the traditional scheme of composition and distribution of potential vegetation in Tenerife (Rivas-Martínez *et al.*, 1993; del Arco *et al.*, 2006).

The results also indicate that the original inhabitants of these islands (the Guanches) may have had an even more profound impact on the ecology of the archipelago than previously recognized. We suggest that insights such as these, provided by long-term ecology, should be taken into account both by evolutionary ecologists and by conservation managers involved in restoration ecology within the archipelago (cf. Willis *et al.*, 2007).

ACKNOWLEDGEMENTS

REFERENCES

Aizpuru, I. & Catalán, P. (1984) Presencia del carpe en la Península Ibérica. *Anales Jardín Botánico de Madrid*, **41**, 143–146.

Anguita, F., Márquez, A., Castiñeiras, P. & Hernán, F. (2002) *Los volcanes de Canarias. Guía geológica e itinerarios*. Rueda, Madrid.

del Arco, M.M., Atienza, E., Atoche, P., del Arco, M.C. & Martín, M. (1997) Dataciones absolutas en la prehistoria de Tenerife. *Homenaje a Celso Martín de Guzmán (1946–1994)*

(ed. by P. Atoche, A. Millares and M. Lobo), pp. 65–77. Universidad de Las Palmas de Gran Canaria, Las Palmas.

del Arco, M.J., Wildpret, W., Pérez, 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*. GRAF-CAN, Santa Cruz de Tenerife.

Arévalo, J.R. & Fernández-Palacios, J.M. (1998) Regeneration strategies of tree species in the laurel forest of Tenerife (the Canary Islands). *Plant Ecology*, **137,** 21–29.

Arévalo, J.R. & Fernández-Palacios, J.M. (2003) Spatial patterns of trees and juveniles in a laurel forest of Tenerife, Canary Islands. *Plant Ecology*, **165,** 1–10.

Arévalo, J.R. & Fernández-Palacios, J.M. (2007) Tree fall gaps and regeneration composition in the laurel forest of Anaga (Tenerife): a matter of size? *Plant Ecology*, **188,** 133–143.

Arroyo, J., Carrión, J.S., Hampe, A. & Jordano, P. (2004) La distribución de las especies a diferentes escalas espacio-temporales. *Ecología del bosque mediterráneo en un mundo cambiante* (ed. by F. Valladares), pp. 27–67. Ministerio de Medio Ambiente, EGRAF S.A., Madrid.

Axelrod, D.I. (1975) Evolution and biogeography of Madrean–Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden*, **62,** 280–334.

Bahn, P. & Flenley, J.R. (1992) *Easter Island: Earth Island*. Thames & Hudson, London.

Barrón, E. & Peyrot, D. (2006) La vegetación forestal en el Terciario. *Paleoambientes y cambio climático* (ed. by J.S. Carrión, S. Fernández and N. Fuentes), pp. 55–76. Fundación Séneca – Agencia de Ciencia y Tecnología de la región de Murcia, Murcia.

Barrón, E., Muñiz, F. & Mayoral, E. (2003) Aspectos macro-florísticos del Plioceno de Lepe (Cuencas de Guadalquivir, Huelva, España). Consideraciones paleoecológicas. *Boletín de la Real Sociedad Española de Historia Natural*, **98,** 91–109.

Bennett, K.D. (1994) Confidence intervals for age estimates and deposition times in Late-Quaternary sediment sequences. *The Holocene*, **4,** 337–348.

Bennett, K.D. (1996) Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, **132,** 155–170.

Bennett, K.D. (2005) *Documentation for psimpoll 4.25 and pscomb 1.03. C programs for plotting and analysing pollen data*. Quaternary Geology, Department of Earth Sciences, University of Uppsala, Uppsala. Available at http://www.kv.geo.uu.se/psimpoll.html (last accessed 7 July 2006).

Bennett, K.D. & Willis, K.J. (2001) Pollen. *Tracking environmental change using lake sediments*. Vol. 3: *Terrestrial, algal, and siliceous indicators* (ed. by J.P. Smol, H.J.B. Birks and W.M. Last), pp. 5–32. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Bennett, K.D., Tzedakis, P.C. & Willis, K.J. (1991) Quaternary refugia of North European trees. *Journal of Biogeography*, **18,** 103–115.

Bennett, K.D., Boreham, S., Sharp, M.J. & Switsur, V.R. (1992) Holocene history of environment, vegetation and human settlement on Catta Ness, Lunnasting, Shetland. *Journal of Ecology*, **80,** 241–273.

Birks, H.J.B. & Gordon, A.D. (1985) *Numerical methods in Quaternary pollen analysis*. Academic Press, London.

Blanco, E., Casado, M.A., Costa, M., Escribano, R., García, M., Génova, M., Gómez, A., Gómez, F., Moreno, J.C., Morla, C., Regato, P. & Sainz, H. (1997) *Los bosques ibéricos: una interpretación geobotánica*. Editorial Planeta, Barcelona.

Bocherens, H., Michaux, J., García-Talavera, F. & Van der Plicht, J. (2006) Extinction of endemic vertebrates on islands: the case of the giant rat *Canariomys bravoi* (Mammalia, Rodentia) on Tenerife (Canary Islands, Spain). *Comptes Rendus Palevol*, **5,** 885–891.

Bramwell, D. (1976) The endemic flora of the Canary Islands; distribution, relationships and phytogeography. *Biogeography and ecology in the Canary Islands* (ed. by G. Kunkel), pp. 207–240. Junk, The Hague.

Burjachs, F. (2006) Palinología y reconstitución paleoecológica. *Ecosistemas*, **15**. Available at http://www.revistaecosistemas.net/articulo.asp?Id=395.pdf.

Burjachs, F. & Juliá, R. (1994) Abrupt climatic changes during the last glaciation based on pollen analysis of the Abric Romani, Catalonia, Spain. *Quaternary Research*, **42,** 308–315.

Cabrera, J.C. (2001) Poblamiento e impacto aborigen. *Naturaleza de las Islas Canarias: ecología y conservación* (ed. by J.M. Fernández-Palacios and J.L. Martín Esquivel), pp. 241–245. Publicaciones Turquesa, Santa Cruz de Tenerife.

Canals, M., Urgelés, R., Masson, D.G. & Casamor, J.L. (2000) Los deslizamientos submarinos de las Islas Canarias. *Makaronesia*, **2,** 57–69.

Carine, M.A., Russell, S.J., Santos-Guerra, A. & Francisco-Ortega, J. (2004) Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany*, **91,** 1070–1085.

Carracedo, J.C., Day, S., Guillou, H., Badiola, E.R., Canas, J.A. & Torrado, F.J.P. (1998) Hotspot volcanism close to a passive continental margin: the Canary Islands. *Geological Magazine*, **135,** 591–604.

Carracedo, J.C., Pérez Torrado, F.J., Ancochea, E., Meco, J., Hernán, F., Cubas, C.R., Casillas, R., Rodríguez Badiola, E. & Ahijado, A. (2002) Cenozoic volcanism II: the Canary Islands. *The geology of Spain* (ed. by W. Gibbons and T. Moreno), pp. 439–472. Geological Society, London.

Carrión, J.S. (2002) Patterns and processes of Late Quaternary environmental change in a montane region of southwestern Europe. *Quaternary Science Reviews*, **21,** 2047–2066.

Carrión, J.S. (2003) Sobresaltos en el bosque mediterráneo: incidencia de las perturbaciones observables a una escala paleoecológica. *Ecosistemas*, **12**. Available at http://www.revistaecosistemas.net/articulo.asp?Id=189.pdf.

Carrión, J.S. & Dupré, M. (1996) Late Quaternary vegetational history at Navarrés, Eastern Spain. A two core approach. *New Phytologist*, **134,** 177–191.

Carrión, J.S., Andrade, A., Bennett, K.D., Navarro, C. & Munuera, M. (2001a) Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. *The Holocene*, **11**, 635–653.

Carrión, J.S., Munuera, M., Dupré, M. & Andrade, A. (2001b) Abrupt vegetation changes in the Segura Mountains of southern Spain throughout the Holocene. *Journal of Ecology*, **89**, 783–797.

Carrión, J.S., Sánchez-Gómez, P., Mota, J.F., Yll, R. & Chaín, C. (2003a) Holocene vegetation dynamics, fire and grazing in the Sierra de Gádor, southern Spain. *The Holocene*, **13**, 839–849.

Carrión, J.S., Yll, E.I., Walker, M.J., Legaz, A.J., Chaín, C. & López, A. (2003b) Glacial refugia of temperate, Mediterranean and Ibero-North African flora in south-eastern Spain: new evidence from cave pollen at two Neanderthal man sites. *Global Ecology and Biogeography*, **12**, 119–129.

Carrión, J.S., Yll, E.I., Willis, K.J. & Sánchez, P. (2004) Holocene forest history of eastern plateaux in the Segura Mountains (Murcia, southeastern Spain). *Review of Palaeobotany and Palynology*, **132**, 219–236.

Ceballos, L. & Ortuño, F. (1976) *Estudio sobre la vegetación y la flora forestal de las Canarias occidentales*, 2nd edn. Cabildo Insular de Tenerife, Santa Cruz de Tenerife.

Cheddadi, R., Lamb, H.F., Guiot, F. & van der Kaars, S. (1998) Holocene climatic change in Morocco: a quantitative reconstruction from pollen data. *Climate Dynamics*, **14**, 883–890.

Clark, R.L. (1982) Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et Spores*, **24**, 523–535.

Coudé-Gaussen, G. & Rognon, P. (1993) Contrasting origin and character of Pleistocene and Holocene dust falls on the Canary Islands and southern Morocco: genetic and climatic significance. *Geological Society, London, Special Publications*, **72**, 277–291.

Crawley, M.J. & Long, C.R. (1995) Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. *Journal of Ecology*, **83**, 683–696.

Criado, C. (2002) *Breve e incompleta historia del antiguo lago de la ciudad de San Cristóbal de La Laguna*. Concejalía de Cultura y Patrimonio Histórico Artístico, San Cristóbal de La Laguna.

Cronk, Q.C.B. (1992) Relict floras of Atlantic Islands: patterns assessed. *Biological Journal of the Linnean Society*, **46**, 91–103.

Damnati, B. (2000) Holocene lake records in the Northern Hemisphere of Africa. *Journal of African Earth Sciences*, **31**, 253–262.

Diamond, J.M. (2005) *Collapse: how societies choose to fail or survive*. Allen Lane/Penguin, London.

Do Amaral Franco, J. (1990) *Quercus. Flora Ibérica*, Vol. 2 (ed. by G. López), pp. 15–26. Real Jardín Botánico de Madrid, Servicio de Publicaciones del CSIC, Madrid.

Emerson, B.C. (2002) Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process. *Molecular Ecology*, **11**, 951–966.

Emerson, B.C. & Oromí, P. (2005) Diversification of the forest beetle genus *Tarphius* on the Canary Islands, and the evolutionary origins of island endemics. *Evolution*, **59**, 586–598.

Fernández, A.B. (2001) Conservación y restauración ecológica de los bosques. *Naturaleza de las Islas Canarias: ecología y conservación* (ed. by J.M. Fernández-Palacios and J.L. Martín Esquivel), pp. 378–382. Turquesa Editorial, Santa Cruz de Tenerife.

Fernández-Caldas, E., Tejedor, M.L. & Quantin, P. (1982) *Suelos de regiones volcánicas: Tenerife, Islas Canarias*. Secretariado de Publicaciones de la Universidad de La Laguna, Consejo Superior de Investigaciones Científicas, La Laguna.

Fernández-Palacios, J.M. (1992) Climatic responses of plant species on Tenerife, the Canary Islands. *Journal of Vegetation Science*, **3**, 595–602.

Fernández-Palacios, J.M. & Arévalo, J.R. (1998) Tree fall gap characteristics and regeneration in the laurel forest of Tenerife. *Journal of Vegetation Science*, **9**, 297–306.

Fernández-Palacios, J.M. & de Nicolás, J.P. (1995) Altitudinal pattern of vegetation variation on Tenerife. *Journal of Vegetation Science*, **6**, 183–190.

Fernández-Palacios, J.M. & Martín Esquivel, J.L. (2001) *Naturaleza de las Islas Canarias: ecología y conservación*. Turquesa Ediciones, Santa Cruz de Tenerife.

Fernández-Palacios, J.M. & Whittaker, R.J. (2008) The Canaries: an important biogeographical meeting place. *Journal of Biogeography*, **35**, 379–387.

Fernández-Palacios, J.M., Arévalo, J.R., Delgado, J.D. & Otto, R. (2004) *Canarias. Ecología, medio ambiente y desarrollo*. Centro de la Cultura Popular de Canarias, La Laguna.

Francisco-Ortega, J., Santos-Guerra, A., Kim, S.C. & Crawford, D.J. (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. *American Journal of Botany*, **87**, 909–919.

Galván, D. (1993) Los inicios de la deforestación de la Isla de Tenerife y las ordenanzas del cabildo sobre la madera (1497–1532). *Strenae emmanuelae marrero oblatae* (ed. by G. Díaz and F. González), pp. 373–389. Secretariado de Publicaciones de la Universidad de La Laguna, La Laguna.

García-Talavera, F. (1999) La Macaronesia. Consideraciones geológicas, biogeográficas y paleoecológicas. *Ecología y cultura en Canarias* (ed. by J.M. Fernández-Palacios, J.J. Bacallado and J.A. Belmonte), pp. 39–63. Museo de las Ciencias y el Cosmos, Cabildo Insular de Tenerife, Santa Cruz de Tenerife.

Gasse, F. (2000) Hydrological changes in the African tropics since the Last Glacial Maximum. *Quaternary Science Reviews*, **19**, 189–211.

Gómez-Orellana, L., Ramil-Rego, P. & Muñoz, C. (2007) The Würm in NW Iberia, a pollen record from Area Longa (Galicia). *Quaternary Research*, **67**, 438–452.

Grivet, D. & Petit, R.J. (2003) Chloroplast DNA phylogeography of the hornbeam in Europe: evidence for a bottleneck at the outset of postglacial colonization. *Conservation Genetics*, **4**, 47–56.

Herrera, J. (1995) Acorn predation and seedling production in a low-density population of cork oak (*Quercus suber* L.). *Forest Ecology and Management*, **76,** 197–201.

Höllermann, P. (1981) Microenvironmental studies in the laurel forest of the Canary Islands. *Mountain Research and Development*, **1,** 193–207.

Hooghiemstra, H., Stalling, H., Agwu, C.O.C. & Dupont, L. (1992) Vegetational and climatic changes at the northern fringe of the Sahara 250,000–5000 years BP: evidence from 4 marine pollen records located between Portugal and the Canary Islands. *Review of Palaeobotany and Palynology*, **74,** 1–53.

Izquierdo, I., Martín, J.L., Zurita, N. & Arechavaleta, M. (2004) *Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres) 2004*. Gobierno de Canarias, Santa Cruz de Tenerife.

Jalut, G., Amat, A.E., Bonnet, L., Gauquelin, T. & Fontugne, M. (2000) Holocene climatic changes in the Western Mediterranean, from south-east France to south-east Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **160,** 255–290.

Jolly, D., Prentice, I.C., Bonnefille, R., Ballouche, A., Bengo, M., Brenac, P., Buchet, G., Burney, D., Cazet, J.P., Cheddadi, R., Edorh, T., Elenga, H., Elmoutaki, S., Guiot, J., Laarif, F., Lamb, H., Lézine, A.M., Maley, J., Mbenza, M., Peyron, O., Reille, M., Reynaud-Farrera, I., Riollet, G., Ritchie, J.C., Roche, E., Scott, L., Ssemmanda, I., Straka, H., Umer, M., Van Campo, E., Vilimumbalo, S., Vincens, A. & Waller, M. (1998) Biome reconstruction from pollen and plant macrofossil data for Africa and the Arabian peninsula at 0 and 6 ka. *Journal of Biogeography*, **25,** 1007–1028.

Juan, C., Emerson, B.C., Oromí, P. & Hewitt, G.M. (2000) Colonization and diversification: towards a phylogenetic synthesis for the Canary Islands. *Trends in Ecology and Evolution*, **15,** 104–109.

Lamb, H.F. & van der Kaars, S. (1995) Vegetational response to Holocene climatic change: pollen and palaeolimnological data from the Middle Atlas, Morocco. *The Holocene*, **5,** 400–408.

Lamb, H.F., Eicher, U. & Switsur, V.R. (1989) An 18,000-year record of vegetation, lake-level and climatic change from Tigalmamine, Middle Atlas, Morocco. *Journal of Biogeography*, **16,** 65–74.

Lamb, H.F., Damblon, F. & Maxted, R.W. (1991) Human impact on the vegetation of the Middle Atlas, Morocco, during the last 5000 years. *Journal of Biogeography*, **18,** 519–532.

Leiva, M.J. & Fernández-Alés, R. (2003) Post-dispersive losses of acorns from Mediterranean savannah-like forest and shrublands. *Forest Ecology and Management*, **176,** 265–271.

Lomoschitz, A., Meco, J. & Corominas, J. (2002) The Barranco de Tirajana basin, Gran Canaria (Spain). A major erosive landform caused by large landslides. *Geomorphology*, **42,** 117–130.

Machado, M.C. & Ourcival, J.M. (1998) La evolución de la vegetación del norte de Tenerife (Islas Canarias) durante el periodo prehispánico. Aportación antracológica. *Arqueología espacial*, **19–20,** 249–260.

Machado, M.C., del Arco, M.C., Vernet, J.L. & Ourcival, J.M. (1997) Man and vegetation in northern Tenerife (Canary Islands, Spain), during the prehispanic period based on charcoal analyses. *Vegetation History and Archeobotany*, **6,** 187–195.

Magny, M., Miramont, C. & Sivan, O. (2002) Assessment of the impact and anthropogenic factors on Holocene Mediterranean vegetation in Europe on the basis of palaeo-hydrological records. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **186,** 47–59.

Maher, L.J.J. (1972) Nomograms for computing 0.95 confidence limits of pollen data. *Review of Palaeobotany and Palynology*, **13,** 85–93.

Marrero, A. (2004) Procesos evolutivos en plantas insulares, el caso de Canarias. *Island ecology* (ed. by J.M. Fernández-Palacios and C. Morici), pp. 305–356. Asociación Española de Ecología Terrestre y Cabildo de La Palma, Santa Cruz de La Palma.

Marret, F. & Turon, J.L. (1994) Paleohydrology and paleoclimatology off Northwest Africa during the last glacial–interglacial transition and the Holocene: palynological evidences. *Marine Geology*, **118,** 107–117.

Meco, J., Petit-Maire, N., Fontugne, M., Shimmield, G. & Ramos, A.J. (1997) The Quaternary deposits in Lanzarote and Fuerteventura (eastern Canary Islands, Spain): an overview. *Climates of the past* (ed. by J. Meco and N. Petit-Maire), pp. 123–136. Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria.

Milne, R.I. (2006) Northern hemisphere plant disjunctions: a window on Tertiary land bridges and climatic change? *Annals of Botany*, **98,** 465–472.

Moya, O., Contreras-Diaz, H.G., Oromí, P. & Juan, C. (2004) Genetic structure, phylogeography and demography of two ground-beetle species endemic to the Tenerife laurel forest (Canary Islands). *Molecular Ecology*, **13,** 3153–3167.

Nogales, M., Marrero, M. & Hernández, E.C. (1992) Efecto de las cabras cimarronas (*Capra hircus*) en la flora endémica de los pinares de Pajonales, Ojeda e Inagua (Gran Canaria). *Botánica Macaronésica*, **19–20,** 79–86.

Pantaleón-Cano, J., Yll, E.I., Pérez-Obiol, R. & Roure, J.M. (2003) Palynological evidence for vegetation history in semi-arid areas of the western Mediterranean (Almería, Spain). *The Holocene*, **13,** 109–119.

Parsons, J.J. (1981) Human influences on the pine and laurel forests of the Canary Islands. *Geographical Review*, **71,** 253–271.

Peñalba, M.C. (1994) The history of the Holocene vegetation in northern Spain from pollen analysis. *Journal of Ecology*, **82,** 815–832.

Pons, A. & Reille, M. (1988) The Holocene and Upper Pleistocene pollen record from Padul (Granada, Spain): a new study. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **66,** 243–263.

Prentice, I.C., Jolly, D. & BIOME 6000 participants (2000) Mid-Holocene and glacial-maximum vegetation geography of the northern continents and Africa. *Journal of Biogeography*, **27**, 507–519.

Ramil-Rego, P., Muñoz-Sobrino, C., Rodríguez-Guitián, M. & Gómez-Orellana, L. (1998) Differences in the vegetation of the North Iberian Peninsula during the last 16,000 years. *Plant Ecology*, **138**, 41–62.

Rando, J.C. (2002) New data of fossil birds from El Hierro (Canary Islands): probable causes of extinction and some biogeographical considerations. *Ardeola*, **49**, 39–49.

Rando, J.C. & Alcover, J.A. (2008) Evidence for a second western Palaearctic seabird extinction during the last Millennium: the Lava Shearwater *Puffinus olsoni*. *Ibis*, **150**, 188–192.

Rando, J.C., Cabrera, V.M., Larruga, J.M., Hernández, M., Conzález, A.M., Pinto, F. & Bandelt, H.J. (1999) Phylogeographic patterns of mtDNA reflecting the colonization of the Canary Islands. *Annals of Human Genetics*, **63**, 413–428.

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.

Riera, S. (2006) Cambios vegetales holocenos en la región mediterránea de la Península Ibérica: ensayo de síntesis. *Ecosistemas*, **15**, 17–30. Available at http://www.revistaeco-sistemas.net/articulo.asp?Id=401.pdf.

Rivas-Martínez, S., Wildpret, W., del Arco, M., Rodríguez, O., Pérez de Paz, P.L., García-Gallo, A., Acebes, J.R., Díaz, T.E. & Fernández-González, F. (1993) Las comunidades vegetales de la Isla de Tenerife (Islas Canarias). *Itinera Geobotánica*, **7**, 169–374.

Rodríguez-Piñero, J.C. & Rodríguez-Luengo, J.L. (1993) The effect of herbivores on the endemic Canary flora. *Boletin do Museo Municipal do Funchal*, **2**, 265–271.

Rognon, P. (1987) Late Quaternary climatic reconstruction for the Maghreb (North Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **58**, 11–34.

Salas, M. & Cáceres, M.T. (2000) Datos históricos de la presencia de fitónimos relacionados con el género *Quercus* L. en Canarias. *Vegueta*, **5**, 341–347.

Sánchez Goñi, M.F., Eynaud, F., Turon, J.L. & Shackleton, N.J. (1999) High resolution palynological record off the Iberian margin: direct land–sea correlation for the Last Interglacial complex. *Earth and Planetary Science Letters*, **171**, 123–137.

Santos-Guerra, A. (1999) Origen y evolución de la flora Canaria. *Ecología y cultura en Canarias* (ed. by J.M. Fernández-Palacios, J.J. Bacallado and J.A. Belmonte), pp. 107–

129. Museo de las Ciencias y el Cosmos, Cabildo Insular de Tenerife, Santa Cruz de Tenerife.

Sanz de Siria, A. (1987) Datos para el conocimiento de las floras miocénicas de Cataluña. *Paleontología i Evolució*, **21**, 295–303.

Sanz de Siria, A. (1992) Estudio de la microflora oligocena de las cercanías de Cervera. *Treballs del Museo de Geología de Barcelona*, **2**, 269–379.

Sperling, F.N., Washington, R. & Whittaker, R.J. (2004) Future climate change of the subtropical North Atlantic: implications for the cloud forests of Tenerife. *Climatic Change*, **65**, 103–123.

Stevenson, A.C. & Moore, P.D. (1988) Studies in the vegetational history of S.W. Spain. IV. Palynological investigations of a valley mire at El Acebrón, Huelva. *Journal of Biogeography*, **15**, 339–361.

Stockmarr, J. (1971) Tablets with spores used in absolute pollen analysis. *Pollen et Spores*, **13**, 615–620.

Stuiver, M., Reimer, P.J., Bard, E., Beck, J.W., Burr, G.S., Hughen, K.A., Kromer, B., McCormac, G., van der Plicht, J. & Spurk, M. (1998) INTCAL98 radiocarbon age calibration, 24,000–0 cal BP. *Radiocarbon*, **40**, 1041–1083.

Sunding, P. (1979) Origins of the Macaronesian flora. *Plants and islands* (ed. by D. Bramwell), pp. 13–40. Wiley, London.

Sziemer, P. (2000) *Madeira's natural history in a nutshell*. Francisco Ribeiro & Filhos Lda., Funchal.

Turner, C. & Hannon, G.E. (1988) Vegetational evidence for Late Quaternary climatic changes in southwest Europe in relation to the influence of the North Atlantic Ocean. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **318**, 451–485.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (1964) *Flora Europaea*. Cambridge University Press, Cambridge.

Tzedakis, P.C., Lawson, I.T., Frogley, M.R., Hewitt, G.M. & Preece, R.C. (2002) Buffered tree population changes in a Quaternary refugium: evolutionary implications. *Science*, **297**, 2044–2047.

Whitlock, C. & Larsen, C. (2001) Charcoal as a fire proxy. *Tracking environmental change using lake sediments*. Vol. 3: *Terrestrial, algal, and siliceous indicators* (ed. by J.P. Smol, H.J.B. Birks and W.M. Last), pp. 75–97. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977–994.

Willis, K.J. (1994) The vegetational history of the Balkans. *Quaternary Science Reviews*, **13**, 769–788.

Willis, K.J. & Birks, H.J.B. (2006) What is natural? The need for a long-term perspective in biodiversity conservation. *Science*, **314**, 1261–1265.

Willis, K.J., Araújo, M.B., Bennett, K.D., Froyd, C., Figueroa-Rangel, B. & Myers, N. (2007) How can a knowledge of the

past help to conserve the future? Biodiversity conservation strategies and the relevance of long-term ecological studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362,** 175–186.

Wright, H.E. (1967) A square-rod piston sampler for lakesediments. *Journal of Sedimentary Petrology*, **4,** 975–976.

Yll, E.I., Pérez-Obiol, R., Pantaleón-Cano, J. & Roure, J.M. (1997) Palynological evidence for climatic change and human activity during the Holocene on Minorca (Balearic Islands). *Quaternary Research*, **28,** 339–347.

Yll, R., Carrión, J.S., Pantaleón, J., Dupré, M., La Roca, N., Roure, J.M. & Pérez-Obiol, R. (2003) Palinología del Cuaternario reciente en la Laguna de Villena (Alicante, España). *Anales de Biología*, **25,** 65–72.

BIOSKETCH

Lea de Nascimento is a post-graduate student at the University of La Laguna, with a first degree in biology. She is interested in most aspects of island ecology, especially those related to the vegetation of the Canary Islands. She is now working on a palaeoecological study of the sediments of La Laguna (Tenerife) under the supervision of K.J.W. and J.M. F.-P., and will use this work as a part of her PhD. The authors of this paper have varied research interests, but share a common interest in further detailed study of the long-term ecology of the Canary Islands, which will provide useful insights into the various disciplines in which they work individually.

Editor: Jens-Christian Svenning