100 YEARS Journal of Ecology
British Ecological Society

Journal of Ecology 2013, **101**, 368–377 doi: 10.1111/1365-2745.12051

The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change

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Summary

1. Garajonay National Park in La Gomera (Canary Islands) contains one of the largest remnant areas of a forest formation once widespread throughout Europe and North Africa. Here, we aim to address the long-term dynamics (the last 9600 cal. years) of the monteverde forest (laurel forest and *Morella-Erica* heath) located close to the summit of the National Park (1487 m a.s.l.) and determine past environmental and human impacts.

2. We used palaeoecological (fossil pollen, microscopic and macroscopic charcoal) and multivariate ecological techniques to identify compositional change in the monteverde forest in relation to potential climatic and human influences, based on the analysis of a core site at 1250-m elevation.

3. The regional mid-Holocene change towards drier conditions was matched in this system by a fairly rapid shift in representation of key forest elements, with declines in Canarian palm tree (*Phoenix canariensis*), Canarian willow (*Salix canariensis*) and certain laurel forest taxa and an increase in representation of the *Morella–Erica* woody heath.

4. Charcoal data suggest that humans arrived on the island between about 3000 and 1800 years ago, a period of minimal vegetation change. Levels of burning over the last 800 years are among the lowest of the entire 9600 years.

5. *Synthesis*. A rapid climatic-induced shift of forest taxa occurred 5500 years ago, with a decrease in hygrophilous species in the pollen record. In contrast, we found no evidence of a significant response to human colonization. These findings support the idea that Garajonay National Park is protecting a truly ancient relict, comprising a largely natural rather than cultural legacy.

Key-words: Canary Islands, climate change, forest management, historical ecology, Holocene, island ecology, La Gomera, monteverde, palaeoecology and land-use history, Quaternary

Introduction

One of the most pressing global environmental concerns is to determine the range of biodiversity responses to a warmer climate (IPCC 2007). It is widely acknowledged that some regions of the world will be particularly sensitive to global climatic changes (Jónsdóttir *et al.* 2005), but it is uncertain how sensitive many remote island systems may be. In this context, the Canary Islands are of particular interest because they are located in a potentially informative position with respect to the Hadley Circulation (Sperling, Washington & Whittaker 2004).

The Canaries are part of the Atlantic island biogeographical region of Macaronesia (with the Azores, Madeira, Selvagens, and Cape Verde) (Fig. 1) and share biogeographical affinities with the Mediterranean and Northwest Africa. Tree-dominated vegetation types on the Canary Islands include Canarian pine woodland (covering 60 678 ha), thermophilous forest (6432 ha), Canarian palm community (1845 ha), Canarian willow community (429 ha) and monteverde forest (10 181 ha) (del Arco *et al.* 2010): the latter being one of the most biologically distinct ecosystems in Macaronesia. The monteverde forest comprises endemic evergreen laurel forest (broadleaved forest) and *Morella* (formerly *Myrica*)-*Erica* woody heath (ericaceous forest). Associated with the zone of orographic cloud formation, this dense forest, with trees 30 m

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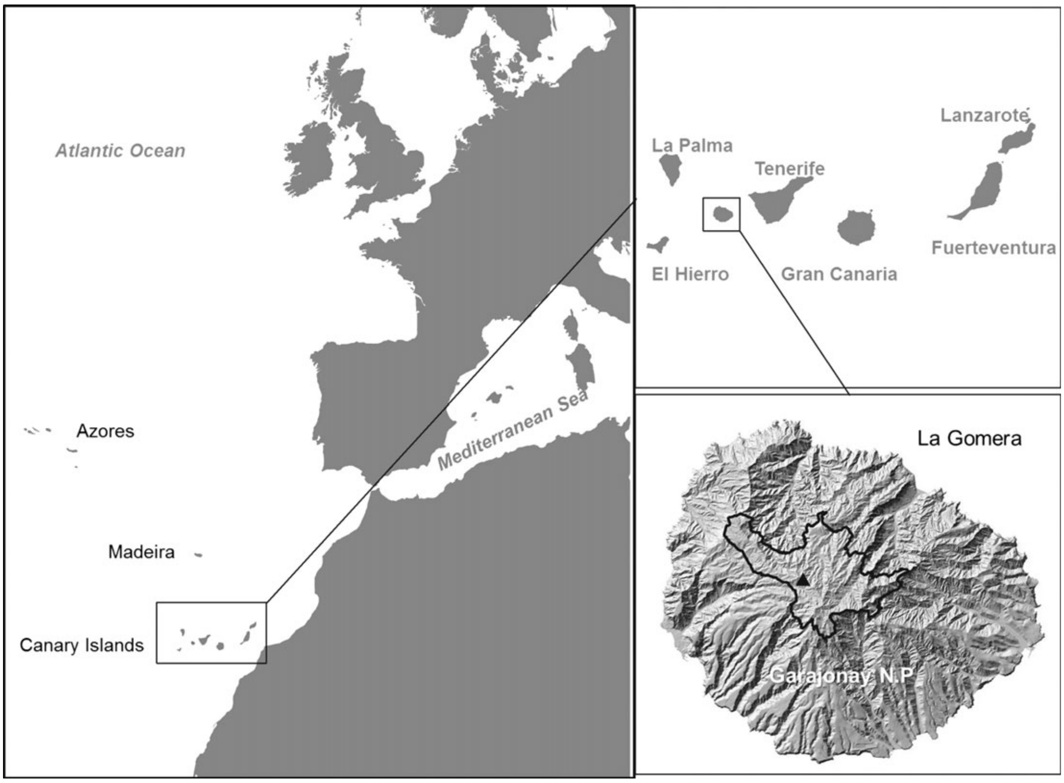

Fig. 1. Map of the location of the coring site (triangle) in Garajonay National Park, La Gomera (Canary Islands).

high, has a complex biogeographical history. It is considered to be a Tethyan relictual flora that colonized from the Mediterranean region during the late Tertiary period and which subsequently went extinct from the Mediterranean region due to the onset of the ice age and the Mediterranean (summer drought) climate (Bramwell 1976; Nakamura *et al.* 2000; Rodríguez-Sánchez & Arroyo 2008; Postigo Mijarra *et al.* 2009; Fernández-Palacios *et al.* 2011). Monteverde forest found refuge in the Macaronesian archipelagos where year-round warm, humid conditions persisted (Santos, 1990). Of the estimated natural extent prior to human colonization, currently only 12.5% of this broadleaved forest remains, mainly in La Gomera (Garajonay National Park) and Madeira (Fernández-Palacios & Whittaker 2008; Fernández-Palacios *et al.* 2011). These forests provide crucial habitat for much of the endemic Canarian avian and invertebrate fauna (Martín *et al.* 2000; Oromí *et al.* 2009) and also play an important role in watershed protection and erosion control (Gómez & Fernández 2009; Rodríguez-Rodríguez *et al.* 2009).

Archaeological estimates of the timing and extent of human migration and settlement in the Canaries are not well constrained. Based on fossil charcoal data from the La Laguna sedimentary sequence (Tenerife), it appears that human arrival (the Guanches) occurred on Tenerife *c.* 2000 years ago (de Nascimento *et al.* 2009). Evidence from archaeological studies suggests human colonization occurred around 2500 years ago (cf. Rando *et al.* 1999; Maca-Meyer *et al.* 2004; Arnay-de-la-Rosa *et al.* 2009). Elsewhere in Macaronesia, human colonization in the Azores occurred as late as the fifteenth century (AD 1432) (Johnson 1994), following which the monteverde formation, which had formerly covered the islands, was drastically reduced, with an apparent collapse in distribution of the small endemic tree *Juniperus brevifolia* and at least two plant species extinctions on Pico island (Connor *et al.* 2012). On the Canaries, a similar situation occurred rather earlier; from 4700 to 2000 cal. years BP, the fossil pollen data from La Laguna (Tenerife) showed the former presence of two tree taxa; *Quercus* and *Carpinus*, not previously considered native to the archipelago, alongside components of the present-day monteverde (de Nascimento *et al.* 2009). These elements declined and disappeared following human colonization and subsequent land-use change on Tenerife.

The extent and impact of Holocene climate changes on the Macaronesian islands is not fully understood. In the Azores, palaeoecological studies (Björck *et al.* 2006) indicate that although there have been climatic fluctuations during the Holocene (last *c.* 12 000 years), the climate has been stable for the last 6000 years (Björck *et al.* 2006). In contrast, recent work to reconstruct past climatic change in the Canary archipelago has indicated a synchronicity with the palaeoclimate in Africa over the last 50 000 years (Ortiz *et al.* 2006). This is understandable, as the eastern Canary Islands lie around 95 km from the African coast (60 km during the Last Glacial Maximum). Evidence from northern African lake sediments suggests a shift from a humid Early-Mid Holocene period to a warmer and drier Mid-Late Holocene (Hooghiemstra *et al.* 1992; deMenocal *et al.* 2000; Ortiz *et al.* 2006; Kröpelin *et al.* 2008). Thus, although traditionally these islands have been considered well-buffered from past climate change, concern has been raised as to the viability of the forest formations in the event of a substantially warmer future world and in the context of extensive contemporary human transformation of these insular landscapes (Ávila *et al.* 2008; Carine & Schaefer 2010; Triantis *et al.* 2010).

In this study, we use fossil pollen, microscopic and macroscopic charcoal (proxies for local and regional fire regime) time series to determine the timing and nature of vegetation shifts and to infer their relationships to climate and human colonization, based on a sedimentary sequence from a coring site within Garajonay National Park. This Park harbours one of the largest continuous areas of monteverde in Macaronesia and contains almost half of the remaining monteverde in the Canary Islands. Human transformation of island ecosystems has been responsible for a high proportion of historically recorded extinctions, and many island species and ecosystems remain under threat (Whittaker & Fernández-Palacios 2007; Prebble & Dowe 2008). In the present context, determining the sensitivity of the Canarian vegetation formations to past human impacts and climate change may provide invaluable insights concerning future environmental change processes (cf. IPCC 2007).

Materials and methods

STUDY SITE

La Gomera lies to the west of Tenerife, and is one of seven main islands that make up the Canary Islands. It rises to almost 1500 m a.s.l. and is one of the smallest of the main islands (378 km^2) of the archipelago. The study site is located in Garajonay National Park and is situated in the centre of the island (Fig. 1). This Park was created to protect the monteverde, which covers an area of 3894 ha and was declared a World Heritage Site by UNESCO in 1986 (UNEP 2011).

Laurel forest and *Morella-Erica* woody heath (monteverde forest) cover 70% of the Garajonay National Park. Monteverde in La Gomera is found between 600 and 1300 m a.s.l. (Fernández & Moreno 2004; del Arco *et al.* 2006; Patiño & González-Mancebo 2011) growing on the humid northern slopes, or slopes covered by clouds (Höllermann 1981). The most common trees are Lauraceae species (*Apollonias barbujana*, *Laurus novocanariensis*, *Ocotea foetens*, and *Persea indica*) with *Ilex canariensis*, *Ilex perado, Picconia excelsa, Rhamnus glandulosa* and *Viburnum rigidum* (del Arco *et al.* 2006).

Above 1300 m a.s.l., the forest is dominated by *Morella faya*, and this forest type is found particularly on cooler summit and central areas. *Morella faya* and the tree heathers *Erica arborea and Erica scoparia* are considered to be shade-intolerant and pioneer species (regeneration primarily by seedlings). They are producers of abundant small seeds, which remain viable in the seed bank for a long time as they cannot germinate under the shade of closed forest canopies (Fernández-Palacios & Arévalo 1998). Moreover, *Morella faya* is an important nitrogen-fixer (Vitousek & Walker 1989).

Small fragments of pine forest are found below the southern ecotone of *Morella* forest (between 1000 and 1200 m a.s.l.). These fragments are dominated by *Pinus canariensis* and *Chamaecytisus proliferus* (del Arco *et al.* 2006). Thermophilous forest occurs between 400 and 600 m a.s.l. on the northern slopes, forming a transition zone with the monteverde, and between 400 and 1200 m a.s.l. on the south slopes below the pine forest. This forest is characterized by the presence of *Juniperus turbinata* subsp. *canariensis*, *Olea cerasiformis* and *Pistacia atlantica*. There are two hygrophilous tree species currently associated with streams and water bodies: *Phoenix canariensis* (Canary palm tree) and *Salix canariensis* (Canary willow). *Phoenix canariensis* occurs from sea level to 1000 m a.s.l. and is particularly associated with debris flows and ravines. *Phoenix canariensis* also grows with willow groves in ravine beds where water runs almost constantly. *Salix canariensis* in La Gomera is found together with monteverde in cleared areas (del Arco *et al.* 2006). The climate at the study site is classified as humid Mediterranean with a mean annual precipitation of 625 mm and mean annual temperature of 13.5 °C (Marzol & Sánchez 2009). Cloud banks occur from 840 m to 1560 m a.s.l., forming a dense fog whose incidence controls the composition and structure of the monteverde (Fernández-Palacios & de Nicolás 1995).

PALAEOECOLOGICAL METHODS

A 6.6-m clay sedimentary sequence (see Fig. S1 in Supporting Information) was collected from La Laguna Grande, a former lake in the basin of an old crater located at 1250 m a.s.l., close to the summit of the Garajonay National Park (28°07′N, 17°15′W) (Fig. 1). This small basin (3 ha) does not contain standing water at the present time, and there is no evidence of agricultural activities. Vegetation around the coring site is composed of *Morella-Erica* woody heath and *Ilex canariensis*.

We used automatic rotation drilling equipment provided by 'Estudios del Terreno S.L.' to collect the sediment sequence. The first 0.5 m of the sedimentary sequence was obtained from the same site and was sampled by hand from the side of a pit in order to avoid distortion or compaction. The core was then transported and stored at the 'Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias' at the University of La Laguna, Tenerife, Spain. The whole sequence was sub-sampled at 2-cm intervals and subsequently analysed in the Long-term Ecology Laboratory, University of Oxford. To reconstruct the vegetation dynamics, a total of 36 samples were processed using 1 cm^3 of sediment, following the standard procedures (Bennett & Willis 2001), involving the addition of acids to remove the carbonates, of alkali to remove humic acids and of hydrofluoric acid to remove silica and silicates. Exotic *Lycopodium* tablets of a known concentration were added in order to determine the concentration of pollen and microfossil charcoal (Stockmarr 1971). From the 6.6 m of material, the first 82 cm yielded fossil pollen (the top 10 cm was discarded).

Slides were mounted with silicon oil for identification and counting. To ensure a statistically significant sample size, 1 to 5 slides were counted for each level until a minimum of 300 pollen grains were recorded. Fern and fungal spores were also identified and counted. Identification of the pollen was carried out using Reille (1995) and the pollen reference material from Europe, Africa and Canary Islands in the collection of the Long-term Ecology Laboratory. In specific cases, we determined to species levels by inferring from the current native and endemic species in La Gomera (Table 1).

All terrestrial pollen types were converted to percentage of total pollen sum based on the sum of total terrestrial pollen, excluding spores and aquatic pollen types. Ferns, fungal spores and aquatic pollen types were expressed as percentages by reference to the total pollen sum. We constructed a percentage pollen diagram using PSIMPOLL version 4.26 (Bennett 2008).

Regional and local fire history was reconstructed through the measurement of micro- (< 150 μm) and macro-charcoal (> 150 μm), respectively. Micro-charcoal was analysed via the routine pollen

Table 1. Information on the main fossil taxa represented in this study, as inferred based on contemporary vegetation ecology and species lists from del Arco *et al.* (2010)

Genera	Species in La Gomera	Distribution (m a.s.l)	Ecology
Erica	*Erica arborea* *Erica platycodon*	500–1400 800–1100	Present in most communities of monteverde: humid monteverde, *Morella-Erica* heath, *Morella* high-elevation forest and dry monteverde
Ilex	*Ilex canariensis* *Ilex perado*	500–1400 800–1300	Present in the dry monteverde, in steep slopes and crests with *Erica platycodon*, in *Morella-Erica* substitution heath and in humid monteverde
Lauraceae	*Laurus novocanariensis**	800–1200	Present in hygrophilous and humid monteverde, in *Erica* heath of windy crests and in *Morella* high-elevation forest
Morella (former *Myrica*)	*Morella faya**	500–1400	Present in most communities of monteverde: humid monteverde, *Erica* heath of windy crests, *Morella-Erica* substitution heath, *Morella* high-elevation forest and dry monteverde
Phoenix	*Phoenix canariensis**	100–1100	Edaphic community
Picconia	*Picconia excelsa**	500–800	Present in the dry monteverde
Prunus	*Prunus lusitanica**	800–1200 (Tenerife)	No description for La Gomera
Salix	*Salix canariensis**	400–1400	Edaphic community

*Indicates the species inferred to be present within this study.

analysis (Whitlock & Larsen 2001), and the charcoal concentration (cm^2 cm^{-3}) in each sample was determined using the point count method (Clark 1982). Macro-charcoal was extracted from 1 cm^3 subsamples using standard charcoal extraction methods and counted using a light microscope (particle cm^{-3}) (Whitlock & Larsen 2001).

Six samples from the core were dated using ^{14}C Accelerator Mass Spectrometry carried out at the 14 CHRONO Centre at Queen's University, Belfast. Calibration of the radiocarbon dates and age-depth modelling were undertaken using R (R Development core team 2011) and routine Clam (Blaauw 2010). All dates were calibrated, using the IntCal09 calibration curve (Reimer *et al.* 2009), to years before present (cal. years BP), with the present defined as 1950.

DETECTING VEGETATION TRANSITIONS RELATED TO CLIMATE AND HUMAN CHANGES

To identify whether there were significant transitions in our vegetation time series and when these shifts occurred, we used numerical zonation of the pollen data using optimal splitting based on information content assessed by the 'broken stick' model (Bennett 1996) (Fig. 2). This analysis was carried out using Psimpoll version 4.26 software. Second, we used the peaks of macro-charcoal, which indicate local occurrence of fire, as an independent proxy to identify human activities.

We used analysis of similarity (Bray–Curtis dissimilarities) to compare the vegetation composition ±200 years either side of the split thus identified in the vegetation series and those based on the peaks of macro-charcoal. We followed these steps:

1. According to the depth–age model, our data are not equally spaced in time; we, therefore, interpolated the pollen data at a constant time-step of 20 years.
2. We used a temporal window of 200 years before and after the shift and the macro-charcoal peaks, involving a total of 20 data points and 400 years. Such a temporal resolution allows us to contrast the composition before and after the transition, taking account of the likely time lag involved when the dominant life forms are long-lived trees.
3. The overall significance of the difference was assessed using one-way permutational ANOVA (PERMANOVA: Anderson, Gorley & Clarke 2008). Pseudo-*F* was calculated from Bray–Curtis distances and the *P*-value obtained using 9999 permutations applying a Monte Carlo test. Similarity percentage analysis (SIMPER) reveals specific taxa that accounted for the greatest differences. PRIMER 6 with PERMANOVA+ software was used to perform both analyses.

Results

CHRONOLOGY AND RESOLUTION

Sediment deposition in La Laguna Grande presents a clearly resolved temporal sequence with a possible hiatus at 36 cm. The sedimentary record appears to extend back to 9600 cal. years BP.

The sedimentation rate varies between 0.003 and 0.04 cm $year^{-1}$. The model indicated that vegetation was reconstructed at an average resolution of one sample every *c.* 125.34 years (see Fig. S2 and Table S1).

FOREST DYNAMICS FOR THE LAST 9600 YEARS: DETECTING VEGETATION TRANSITIONS

Using the depth–age model and pollen zonation, we detected a statistically significant vegetation transition around 5500 cal. years BP (Fig. 2). The two pollen zones determined by optimal splitting are named according to the dominant taxa for each zone.

Zone 1: High abundance of Phoenix canariensis and *Salix canariensis* (9600–5500 cal. years BP)

In this period, dominant taxa in the pollen record include two hygrophilous taxa, *Phoenix canariensis* and *Salix canariensis*,

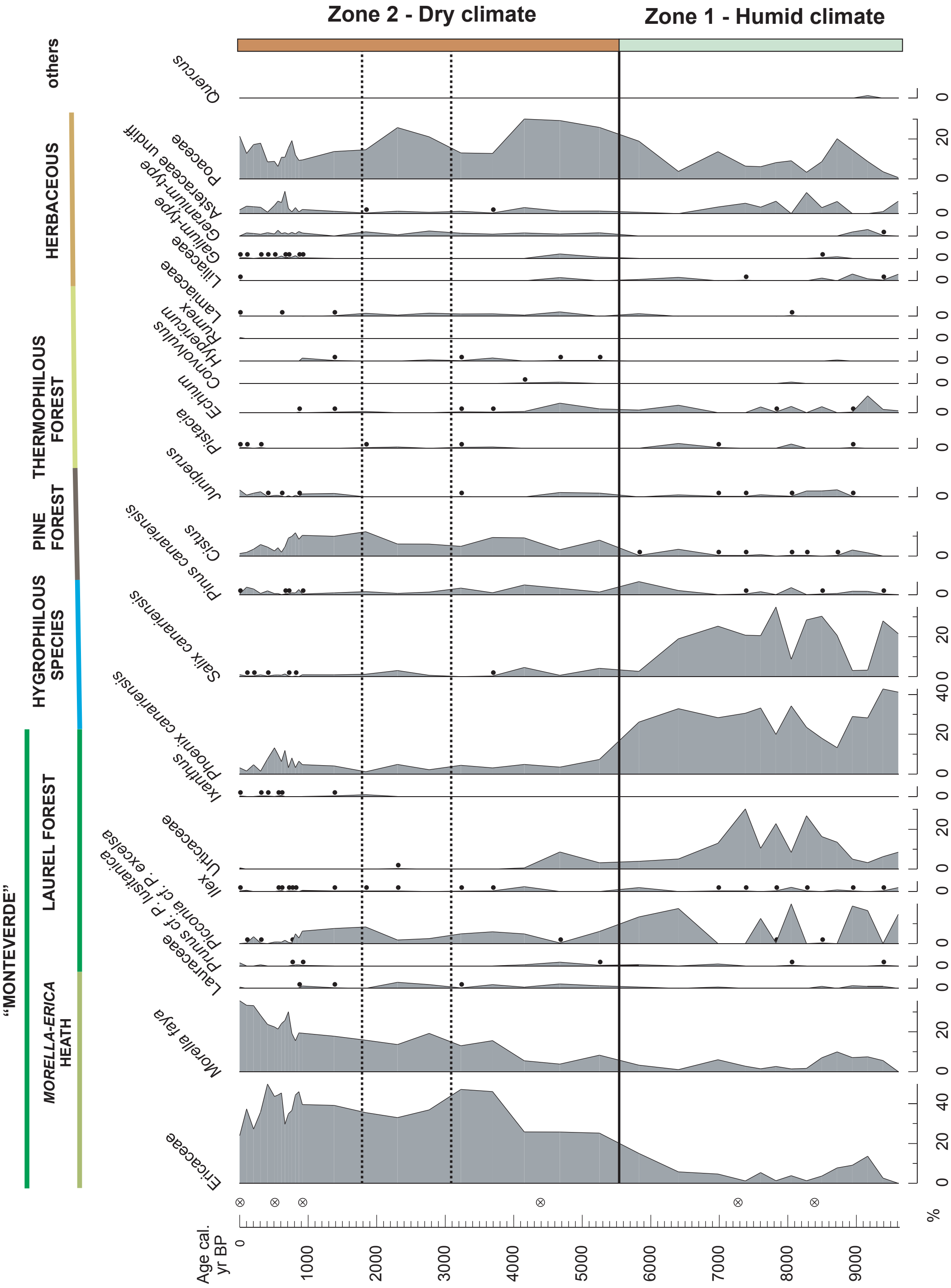

Fig. 2. Pollen diagram of monteverde forest, hygrophilous, thermophilous taxa and grasses in Garajonay National Park, La Gomera. Additional taxa not reaching 0.5% of the total pollen sum are shown in Fig. S3. Ages are calibrated years BP. The pollen boundary is delineated with a solid line according to the optimal splitting option available in PSIMPOLL. The dates where the macro-charcoal peaked are denoted using broken lines.

and two laurel forest taxa, *Picconia excelsa* and Urticaceae (e.g., *Gesnouinia*). *Salix canariensis* greatly decreases in abundance (%) at 5800 cal. years BP. Some taxa are more abundant in the older part of the zone: these include *Erica* and *Morella faya*. *Quercus* (known from mid-Holocene pollen records at La Laguna on Tenerife) appeared at around 9000 cal. years BP, but only four pollen grains were recorded. Taxa we interpret as being thermophilous taxa that have high percentages in this zone include *Echium* and *Pistacia*. *Juniperus* is also present in this period. In terms of herbaceous taxa, Poaceae and Asteraceae are predominant, together with Liliaceae (Fig. 2). Although ferns are present, the percentages remain lower compared with the following zone. Fungal spores remained low in abundance (Fig. 3, see Fig. S3).

Zone 2: Increase of Morella–Erica woody heath (5500 cal. years BP to present)

In this zone, the pollen count is dominated by *Morella faya* and *Erica*, with high values also typical for Poaceae (Figs 2 and 3). Taxa from the monteverde forest include Lauraceae, *Ixanthus viscosus, Picconia excelsa*, *Prunus lusitanica* and Urticaceae, but the values for these taxa of the laurel forest proper are generally low. The two previously prominent hygrophilous taxa, *Phoenix canariensis* and *Salix canariensis,* decrease dramatically and then remain at comparatively low levels throughout the remainder of the core. Thermophilous taxa, such as *Echium* and *Hypericum,* are scarce or even absent. *Pinus canariensis* and *Juniperus* remain at a fairly constant low level of importance, and *Cistus* increases in this zone (Fig. 2). The herbaceous element includes Asteraceae, *Galium*, *Geranium* and Lamiaceae. Ferns present in this zone include *Davallia*, *Polypodium* and *Ophioglossum*. Fungal spores become relatively important over the last 400 years. *Sporormiella,* although remaining low in abundance throughout the sequence, peaked at 900 cal. years BP (Fig. 3b, see Fig. S3).

FIRE HISTORY: DETECTING HUMAN IMPACTS

Results from the macro- and microfossil charcoal analyses suggest that the area surrounding La Laguna Grande has been subjected to fire events during the last 7000 years (Fig. 3c). Regional fires remain low in all samples of the core, with the highest values recorded at 4800 cal. years BP (Fig. 3c). Local fires increase over the last 3600 years, with two large peaks at *c*. 3100 and 1800 cal. years BP, and then an abrupt fall to very low levels over the last *c*. 900 years.

VEGETATION TRANSITIONS RELATED TO CLIMATE AND HUMAN CHANGES

SIMPER analysis revealed which taxa accounted for the greatest observed differences detected by the zone boundary at 5500 cal. years BP. The PERMANOVA analysis of composition 200 years before and after this boundary confirmed this threshold as marking a significant (PERMANOVA: pseudo-$F = 57.2$, P (MC) < 0.01) compositional change marked by an average dissimilarity of 15%. Vegetation differentiation for the taxa contributing more than 5% of the average Bray–Curtis similarity was driven primarily by a decrease in *Phoenix canariensis* (20.82%), *Picconia excelsa* (8.12%), *Pinus canariensis* (5.82%) and the increase in *Erica* (11.30%), ferns (11.07%), *Cistus* (8.49%), Poaceae (7.67%) and *Morella faya* (5.57%) (Table 2, see Table S2).

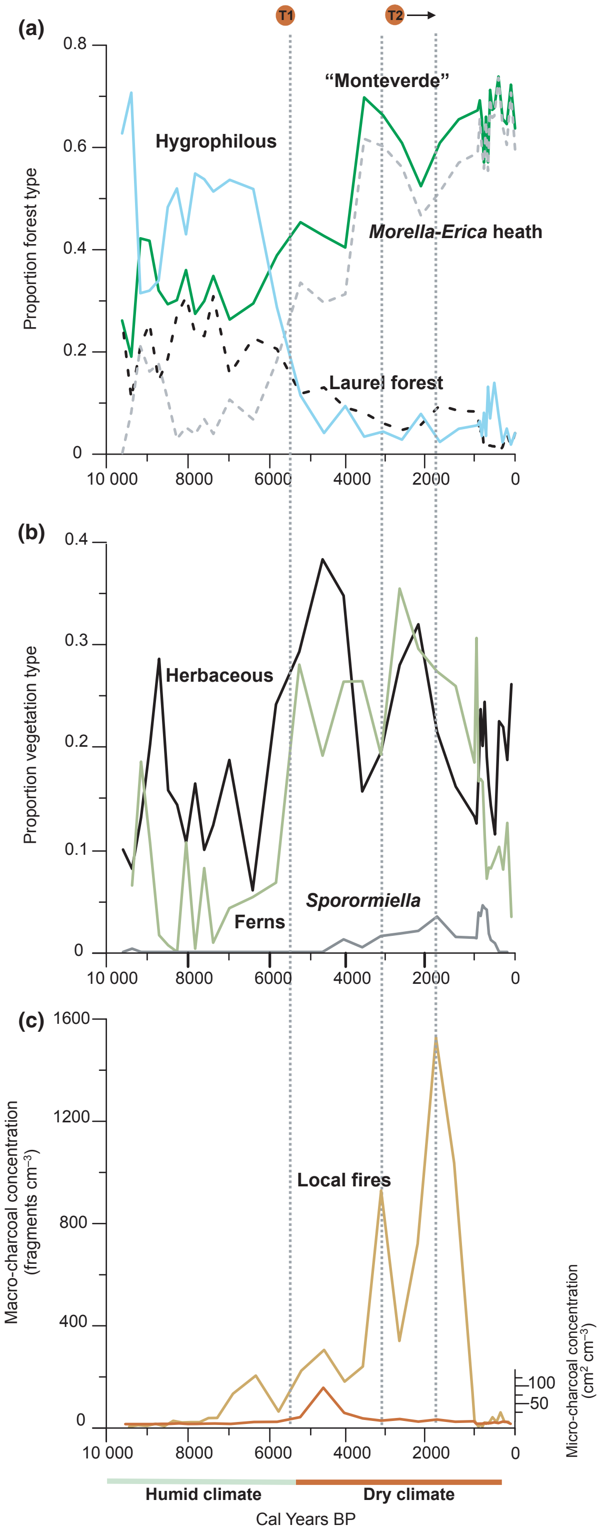

Fig. 3. Pollen percentages for selected vegetation types at Garajonay National Park. (a) Monteverde forest (laurel forest and *Morella-Erica* heath) and hygrophilous taxa; (b) herbaceous, ferns and *Sporormiella*; (c) Charcoal concentration (macro- and micro-charcoal) in particles cm^{-3} and cm^{2} cm^{-3}. T1 (climatic change) and T2 (potential human impact).

Based on the fire history analysis, we identified two peaks that may be related to potential human activities: at 3100 and 1800 cal. years BP. According to the PERMANOVA analysis, the average composition dissimilarity for ±200 years around the two peaks showed a significant composition change (P (MC) < 0.01) with an average dissimilarity of 9%

Table 2. SIMPER results for a time window of ±200 years either site of the vegetation split (at 5500 cal. years BP) and at the two macro-charcoal peaks (at 3100 and 1800 cal. years BP) for a selected group of taxa. permanova P-values and significance are given. Arrows show the direction of change of the proportional contributions of each taxon from the SIMPER analysis. Ages (years) were given in cal. years BP

	Natural (pollen data zonation)		Human (charcoal peaks)			
	5500 cal. years BP (*Pseudo-F* = 57.2)*		3100 cal. years BP (*Pseudo-F* = 57.3)*		1800 cal. years BP (*Pseudo-F* = 17.3)*	
Taxa	Contrib. (%)	Trend post	Contrib. (%)	Trend post	Contrib. (%)	Trend post
Erica	11.30	↑	18.55	↓	13.54	↑
Cistus	8.49	↑	–	–	6.28	↑
Ferns	11.07	↑	28.81	↑	2.04	=
Morella faya	5.57	↑	11.19	↑	8.62	↑
Picconia excelsa	8.12	↓	4.26	↓	8.03	↑
Pinus canariensis	5.82	↓	3.59	↓	–	–
Phoenix canariensis	20.82	↓	3.98	↓	4.85	=
Poaceae	7.67	↑	14.61	↑	18.21	↓

*P (MC) < 0.01.

(Pseudo-$F = 57.26$) and 5% (Pseudo-$F = 17.31$), respectively. Vegetation differentiation in either side of the first peak (3100 cal. years BP) reflects a decrease in *Erica* (18.55%) and an increase in ferns (28.81%), Poaceae (14.61%) and *Morella faya* (11.19%). In relation to the second peak, occurring at 1800 cal. years BP, Poaceae (18.21%) exhibited a decrease while *Erica* (13.54%), *Morella faya* (8.62%), *Picconia excelsa* (8.03%) and *Cistus* (6.28%) increased (Table 2 and Fig. 3, see Table S2).

Discussion

CROSSING A CLIMATIC THRESHOLD: EVIDENCE OF A SHIFT TO DRIER ENVIRONMENTAL CONDITIONS 5500 YEARS AGO

At present, it remains unclear from other palaeoclimatic work in Macaronesian islands whether, how and to what extent they have been affected by climate change during the Holocene. In general, however, there is agreement that at this latitude, in West Africa and the eastern Atlantic, during the Early Holocene (10 000–6000 years ago) conditions were wetter (Hooghiemstra *et al.* 1992; Prentice *et al.* 2000). For example, the end of the African Humid Period (deMenocal *et al.* 2000) is one of the most prominent environmental changes of the past 10 000 years (Kröpelin *et al.* 2008). It represented the transition about 5500 years ago from a 'green Sahara', with the presence of humid-adapted species from tropical forest and wooded grasslands, to the Sahara desert (deMenocal *et al.* 2000). Questions remain about regional extent and whether the transition was gradual or abrupt, and which parts of Africa were most impacted.

We have limited evidence for the Mid- to Late-Holocene climate for the Canary Islands. This is partly because of the poor preservation of proxies (e.g., fossil pollen) due to the volcanic nature of the sediments and lack of permanent lakes. However, recent analyses of δ^{18}O from land snails shells from the eastern islands (Lanzarote, Fuerteventura, and Alegranza, La Graciosa and Montaña Clara islets) have been used to infer a decline in humidity during the Late Holocene (Yanes *et al.* 2011). There is evidence to suggest that Mediterranean regions in the Iberian Peninsula (e.g., eastern Betic Mountains) also became increasingly arid during the period 5000 to 4000 cal. years BP, showing coherence with North African palaeoclimatic data (Carrión *et al.* 2003). The general vegetation pattern observed was a decrease in deciduous broadleaved trees and an expansion of the evergreen sclerophyllous taxa (Carrión *et al.* 2001).

La Gomera represents the first Canary island from which a sequence of pollen-bearing sediments covering the greater part of the Holocene has been obtained. Is there evidence of a climatic synchronicity with the North African palaeoclimate data in the Canary Islands? Our results show a monteverde community change at *c.* 5500 years ago (Figs 2 and 3a), involving a compositional shift change of roughly 15% of the average Bray–Curtis dissimilarity.

During this period, there is a shift to greater representation of *Morella–Erica* woody heath and a decrease in laurel forest taxa, and of *Phoenix canariensis* and *Salix canariensis*. Therefore, we infer that from 9600 to 5500 years ago, the monteverde forest at Garajonay National Park landscape was dominated by laurel forest taxa such as *Ilex*, *Picconia excelsa* and Urticaceae. During the same period, two hygrophilous taxa are abundant, *Phoenix canariensis* and *Salix canariensis*. These two species are indicative of wet environmental conditions (del Arco *et al.* 2010) (Figs 2 and 3), suggesting that during the Early Holocene these trees were favoured by a wetter climate, temporarily flooded lakes or more active stream channels. From 5500 years ago onwards, the catchment was dominated by the *Morella–Erica* heath (pioneering and ridge-top trees); we interpret this shift as a response to drier climatic conditions and consequently, the tree canopy opened and grasses (Poaceae) and ferns increased (Figs 2 and 3). Our SIMPER results also provide an answer to the question posed in the introduction on whether the Canarian forests are sensitive to climate changes. *Erica*, *Morella faya*, Poaceae and ferns all show higher representation 200 years after the zone boundary than 200 years before it (Table 2). In contrast, *Phoenix canariensis, Picconia excelsa* and *Pinus canariensis* decreased, reflecting different degrees of responses to climate change. Moreover, *Salix canariensis* began declining 500 years before the dividing point. This decrease in Canarian willow suggests that climate change towards drier conditions in La Gomera may have started earlier in time. Thus, we consider that the vegetation composition during this period of time (6000–5500 cal. years BP) may be a transition state towards the current vegetation composition. In short, our pollen data are consistent with a marked change in vegetation composition over a roughly 400-year period, in response to a significant shift in climate, but we cannot be sure from these data whether the climate change was swift or a gradual transition, and thus, we cannot be sure either of how quickly the vegetation responded to the changing climate.

Long-term data on fire events also suggest a climatic shift as regional fires (micro-charcoal concentration) reached their maximum at 4800 cal. years ago, followed by an increase in local fires at about 3000 cal. years BP (macro-charcoal concentration). These results add new pieces to the Macaronesian palaeoecological puzzle and provide the first evidence to suggest that the shift towards a drier mid-Holocene climate may be traced in the Canary Islands. Although certainly affecting individual species (Fig. 2 and Table 2), this change was not sufficient to lead to very dramatic vegetation transitions at the site, which remained embedded within a forested landscape throughout.

EVIDENCE OF FIRST HUMAN COLONIZATION

One of the principal reasons for the Park's World Heritage status is the sheer size of the monteverde forest, which covers a large continuous area of the Garajonay National Park (UNEP 2011). The most recent palaeoecological study carried out in the Canaries showed that the first inhabitants of Tenerife (the Guanches) changed the composition of the forest and even caused the extinction of at least two tree species (de Nascimento *et al.* 2009). So, what impact did the first people have on the forests of La Gomera?

Generally, human arrival in new regions generates at least some detectable palaeoecological changes: extinction of some taxa, proliferation of grasses, increase of charcoal particles, typically coinciding with an increase in fungal spores (e.g., *Sporormiella*), indicative of grazing activities. In contrast to other palaeoecological studies in Macaronesia (e.g., Tenerife and several islands in the Azores), our results indicate that Garajonay National Park was not heavily impacted by human colonization: assuming it occurred sometime between 3100 and 1800 years ago, as we infer. This is supported by the low SIMPER values on both macro-charcoal peaks (9% and 5%, respectively). In addition, there is no evidence from the pollen record that indicates extinction of any tree taxa. The low frequency of *Quercus* (four pollen grains) and short period of presence in the core fail to distinguish between presence on La Gomera and longer-distance pollen transport.

Although archaeological studies have identified that the aborigines arrived on the Canary Islands around 2500 years ago, it is unclear how many human influxes occurred after initial settlement and prior to the Hispanic contact in the fifteenth century (Rando *et al.* 1999). In our La Gomera core, the first big peak in macro-charcoal at around 3100 cal. years BP raises the hypothesis that humans had colonized by this time. The slight rise in *Sporormiella* spore concentration in this period provides limited additional support for this. Moreover, the increase in ferns and Poaceae 200 years after the peak in fire suggest an opening of the forest, which may have been due to human activities. If this scenario is accepted, then by around 1800 cal. years BP, the timing of the second peak in macro-charcoal, human activity in the vicinity may have been more significant. Notwithstanding, there is no clear evidence of a compositional shift in the pollen data in this period. This is confirmed by our SIMPER analysis, from which *Morella faya* is the only taxa displaying a consistent response in connection with both peaks of fire.

Fire and grazing activities are considered the main threats for the Park (UNEP 2011). In fact, the recent fires in La Gomera (summer 2012) have raised concern about the protection and recovery of this ancient forest. We currently lack contemporary data on post-fire recovery in these forests, and our long-term data may help in filling this gap. Here, we showed that fires have been a feature of this landscape for approximately the last 6000 cal. years but that in general, the levels of burning throughout the last 900 years have been low in the context of our 9600-year record. We also have shown that for the same period (the last 900 years), the levels of *Sporormiella* spores are insufficient to indicate local grazing activities (but see the late spike in the final layers: Fig. S3). Our results therefore suggest that the upland forests of La Gomera have experienced low fire incidence and little human impact since settlement. This is consistent with colonization patterns elsewhere, whereby high-elevation cloud forest sites are the last to be colonized and transformed.

Conclusions

The circumstances of our study site (on a small island, in a small basin and high elevation) and the absence of a strong human impact signal allow us to suggest that global climate changes (e.g., the end of the African Humid period) may be traced on the Canary Islands. Our findings indicate that although the original inhabitants of the Canary Islands and the fifteenth-century Castillian conquest on each had profound impacts on the vegetation of the archipelago, Garajonay National Park is something of an exception. This is important in terms of conservation management as this National Park is protecting one of the largest laurel forest patches and one that is a truly ancient with a predominantly natural legacy.

Acknowledgements

We are greatly indebted to the director of conservation, A.B. Fernández, and rangers from Garajonay National Park for their valuable assistance during the fieldwork. This research was supported by the Spanish Ministry of the Environment and Rural and Marine Environs, Autonomous Organisation of National Parks (project 003/2008), and the Canarian Agency for Research, Innovation and Information for Society and the European Regional Development Fund (project SolSubC200801000053). S.N participated through a postdoctoral fellowship from the Spanish Ministry of Education (EX2009-0669).

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Received 31 July 2012; accepted 27 November 2012
Handling Editor: Matt McGlone

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Sediment description.

Figure S2. Clam results for the depth-age curve for La Laguna Grande core at Garajonay National Park based on ^{14}C dating and calibration.

Figure S3. Additional pollen taxa not shown in Figure 2.

Table S1. Radiocarbon dating of La Laguna Grande at Garajonay National Park.

Table S2. SIMPER results.